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THE ANIMAL MIND



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THE ANIMAL BEHAVIOR SERIES. VOLUME II

THE ANIMAL MIND

A Text-book of Comparative
Psychology

BY

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SECOND EDITION

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PREFACE TO THE FIRST EDITION

THE title of this book might more appropriately, if not more concisely, have been "The Animal Mind as Deduced from Experimental Evidence." For the facts set forth in the following pages are very largely the results of the experimental method in comparative psychology. Thus many aspects of the animal mind, to the investigation of which experiment either has not yet been applied or is perhaps not adapted; are left wholly unconsidered. This limitation of the scope of the book is a consequence of its aim to supply what I have felt to be a chief need of comparative psychology at the present time. Although the science is still in its formative stage, the mass of experimental material that has been accumulating from the researches of physiologists and psychologists is already great, and is also for the most part inaccessible to the ordinary student, being widely scattered and to a considerable extent published in journals which the average college library does not contain. While we have books on animal instincts and on the interpretation of animal behavior, we have no book which adequately presents the simple facts.

Probably no bibliography seems to one who carefully examines it entirely consistent in what it includes and what it excludes. Certainly the one upon which this book is based contains inconsistencies. The design has been to exclude works bearing only upon general physiology, upon the morphology of the nervous system and sense organs, or upon the nature of animal instinct as such, and to include those which bear upon the topics mentioned in the chapter headings. Within these limits, the collection of references upon

no topic is as full as would be necessary for the bibliography of a special research upon that topic. Doubtless there are omissions for which no excuse can be found. In one or two cases, where the literature upon a single point is very large, as for example, in the case of the function of the semicircular canals, only a few of the more important references have been given.

One further comment may be made. The book throughout deals with comparative rather than with genetic psychology.

I gratefully acknowledge help from a number of sources. To Professor Titchener I owe, not only my share of that genuine psychological spirit which he so successfully imparts to his pupils according to their ability, but various helpful criticisms upon the present work, about half of which he has read in manuscript. Dr. Yerkes has given me much invaluable aid in securing access to material, and has very kindly permitted me to see the proofs of his book on "The Dancing Mouse." As editor of the series he has reviewed my manuscript to its great advantage. Professors Georges Bohn and George H. Parker have showed especial courtesy in making their work accessible to me. Professor Jennings has kindly allowed the use of a number of illustrations from his book on "The Behavior of the Lower Organisms." My colleague Professor Aaron L. Treadwell has generously helped me in ways too numerous to specify. But perhaps my heaviest single obligation is to Professor I. Madison Bentley, who has read the manuscript of the entire book, and whose advice and criticism have been of the utmost benefit to every part of it.

M. F. W.

VASSAR COLLEGE, POUGHKEEPSIE, N.Y.

October 1, 1907.

PREFACE TO THE SECOND EDITION

THE advance of comparative psychology during the past nine years has been remarkable. In preparing a second edition of this book I have tried to include every newly discovered fact of the first importance, but the literature is now so extensive that in order to keep the bibliography within reasonable limits, I have had to exercise more selection than I did in preparing the bibliography for the first edition. For like reasons, the text of the book does not enter so fully into detail in describing the results of a particular investigation as was possible when the material at hand was so much less in amount.

More than half the book has been completely rewritten, including the chapters on Vision, on Spatially Determined Reactions, and on The Modification of Conscious Processes by Individual Experience. I hope that the edition represents an advance upon its predecessor, not only by including many newly ascertained facts, but also by presenting its subject matter in more logical form.

M. F. W.

VASSAR COLLEGE, POUGHKEEPSIE, N.Y.,
April, 1917.

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THE ANIMAL MIND

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CHAPTER I

THE DIFFICULTIES AND METHODS OF COMPARATIVE PSYCHOLOGY

§ 1. *Difficulties*

THAT the mind of each human being forms a region inaccessible to all save its possessor, is one of the commonplaces of reflection. His neighbor's knowledge of each person's mind must always be indirect, a matter of inference. How wide of the truth this inference may be, even under the most favorable circumstances, is also an affair of everyday experience: each of us can judge his fellow-men only on the basis of his own thoughts and feelings in similar circumstances, and the individual peculiarities of different members of the human species are of necessity very imperfectly comprehended by others. The science of human psychology has to reckon with this unbridgeable gap between minds as its chief difficulty. The psychologist may look into his own mind and study its workings with impartial insight, yet he can never be sure that the laws which he derives from such a study are not distorted by some personal twist or bias. For example, it has been suggested that the philosopher Hume was influenced by his tendency toward a visual type of imagination in his discussion of the nature of ideas, which to him were evidently visual images. As is well known, the experimental method in psychology has aimed to minimize

the danger of confusing individual peculiarities with general mental laws. In a psychological experiment, an unbiassed observer is asked to study his own experience under certain definite conditions, and to put it into words so that the experimenter may know what the contents of another mind are like in the circumstances. Thus language is the essential apparatus in experimental psychology; language with all its defects, its ambiguity, its substitution of crystallized concepts for the protean flux of actually lived experience, its lack of terms to express those parts of experience which are of small practical importance in everyday life, but which may be of the highest importance to mental science. Outside of the psychological laboratory language is not always the best guide to the contents of other minds, because it is not always the expression of a genuine wish to communicate thought. "Actions speak louder than words," the proverb says; but when words are backed by good faith they furnish by far the safest indication of the thought of others. Whether, however, our inferences are made on the basis of words or of actions, they are all necessarily made on the hypothesis that human minds are built on the same pattern, that what a given word or action would mean for my mind, this it means also for my neighbor's mind.

If this hypothesis be uncertain when applied to our fellow human beings, it fails us utterly when we turn to the lower animals. If my neighbor's mind is a mystery to me, how great is the mystery which looks out of the eyes of a dog, and how insoluble the problem presented by the mind of an invertebrate animal, an ant or a spider! We know that such minds must differ from ours not only in certain individual peculiarities, but in ways at whose nature we can only guess. The nervous systems of many animals vary widely from our own. We have, perhaps, too little knowledge about the

functions of our own to conjecture with any certainty what difference this must make in the conscious life of such animals; but when we find sense organs, such as the compound eyes of insects or crustaceans, constructed on a plan wholly diverse from that of ours; when we find organs apparently sensory in function, but so unlike our own that we cannot tell what purpose they serve, — we are baffled in our attempt to construct the mental life of the animals possessing them, for lack of power to supply the sensation elements of that life. “It is not,” said Locke, “in the power of the most exalted wit or enlarged understanding, by any quickness or variety of thought, to invent or frame one new simple idea in the mind” (418, Bk. II, ch. 2); we cannot imagine a color or a sound or a smell that we have never experienced; how much less the sensations of a sense radically different from any that we possess! Again, a bodily structure entirely unlike our own must create a background of organic sensation which renders the whole mental life of an animal foreign and unfamiliar to us. We speak, for example, of an “angry” wasp. Anger, in our own experience, is largely composed of sensations of quickened heart beat, of altered breathing, of muscular tension, of increased blood pressure in the head and face. The circulation of a wasp is fundamentally different from that of any vertebrate. The wasp does not breathe through lungs, it wears its skeleton on the outside, and it has the muscles attached to the inside of the skeleton. What is anger like in the wasp’s consciousness? We can form no adequate idea of it.

To this fundamental difficulty of the dissimilarity between animal minds and ours is added, of course, the obstacle that animals have no language in which to describe their experience to us. Where this unlikeness is greatest, as in the case of invertebrate animals, language would be of little use

since we could not interpret it from our experience; but the higher vertebrates could give us much insight into their minds if they could only speak. We are, however, restricted to the inferences we can draw from movements and sounds that are made for the most part without the intention of communicating anything to us. One happy consequence of this fact, which to a slight extent balances its disadvantages, is that we have not to contend with self-consciousness and posing, which often invalidate human reports of introspection.

From these general considerations we can understand something of the special difficulties that beset the path of the comparative psychologist, who desires to know the contents of minds below the human level. Knowledge regarding the animal mind, like knowledge of human minds other than our own, must come by way of inference from behavior. Two fundamental questions then confront the comparative psychologist. First, by what method shall he find out how an animal behaves? Second, how shall he interpret the conscious aspect of that behavior?

§ 2. *Methods of Obtaining Facts: The Method of Anecdote*

The reading of such a book as Romanes's "Animal Intelligence," or of the letters about animal behavior in the *London Spectator*, will reveal one method of gathering information about what animals do. This has been termed the Method of Anecdote. It consists essentially in taking the report of another person regarding the action of an animal, observed most commonly by accident, and attracting attention because of its unusual character. In certain cases the observer while engaged in some other pursuit happens to notice the singular behavior of an animal, and at his leisure

writes out an account of it. In others, the animal is a pet, in whose high intellectual powers its master takes pride. It is safe to say that this method of collecting information always labors under at least one, and frequently under several, of the following disadvantages:—

1. The observer is not scientifically trained to distinguish what he sees from what he infers.
2. He is not intimately acquainted with the habits of the species to which the animal belongs.
3. He is not acquainted with the past experience of the individual animal concerned.
4. He has a personal affection for the animal concerned, and a desire to show its superior intelligence.
5. He has the desire, common to all humanity, to tell a good story.

Some of these tendencies to error it is unnecessary to illustrate. A good example of the dangers of (2), lack of acquaintance with the habits of the species, is given by Mr. and Mrs. Peckham. They quote the following anecdote reported by no less eminent and trained an observer than Wundt. "I had made myself," says that psychologist, "as a boy, a fly-trap like a pigeon cote. The flies were attracted by scattering sugar and caught as soon as they had entered the cage. Behind the trap was a second box separated from it by a sliding door, which could be opened or shut at pleasure. In this I had put a large garden spider. Cage and box were provided with glass windows on the top, so that I could quite well observe anything that was going on inside. . . . When some flies had been caught, and the slide was drawn out, the spider of course rushed upon her prey and devoured them. . . . This went on for some time. The spider was sometimes let into the cage, sometimes confined to her own box. But

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one day I made a notable discovery. During an absence the slide had been accidentally left open for some little while. When I came to shut it, I found that there was an unusual resistance. As I looked more closely, I found that the spider had drawn a large number of thick threads directly under the lifted door, and that these were preventing my closing it. . . ."

"What was going on in the spider's mind?" Wundt asks, and points out that it is unnecessary to assume that she *understood and reasoned out the mechanical requirements of the situation*. The whole matter can be explained, he thinks, in a simpler way. "I imagine that as the days went by there had been formed in the mind of the spider a determinate association on the one hand between free entry into the cage and the pleasurable feeling attending satisfaction of the nutritive impulse, and on the other between the closed slide and the unpleasant feeling of hunger and inhibited impulse. Now in her free life the spider had always employed her web in the service of the nutritive impulse. Associations had therefore grown up between the definite positions of her web and definite peculiarities of the objects to which it was attached, as well as changes which it produced in the positions of certain of these objects, — leaves, small twigs, etc. The impression of the falling slide, that is, called up by association the idea of other objects similarly moved which had been held in their places by threads properly spun; and finally there were connected with this association the other two of pleasure and raising, unpleasantness and closing, of the door" (797. pp. 351-352).

The Peckhams remark in criticism of this observation: "Had Wundt been familiar with the habits of spiders, he would have known that whenever they are confined they walk around and around the cage, leaving behind them lines

of web. Of course many lines passed under his little sliding door, and when he came to close it there was a slight resistance. These are the facts. His inference that there was even a remotest intention on the part of his prisoner to hinder the movement of the door is entirely gratuitous. Even the simpler mental states that are supposed to have passed through the mind of the spider were the products of Wundt's own imagination" (572, p. 230). The fact that the anecdote was a recollection of childhood, so that it would probably be impossible to bring any evidence from the character of the web or other circumstance against the suggestion of Mr. and Mrs. Peckham, is a further instance of the unscientific use of anecdotal testimony.

An illustration of the third objection mentioned above, the disadvantage of ignorance of the animal's individual history, is furnished by Lloyd Morgan. In describing his futile efforts to teach a fox terrier the best way to pull a crooked stick through a fence, he says that the dog showed no sign "of perceiving that by pushing the stick and freeing the crook he could pull the stick through. Each time the crook caught he pulled with all his strength, seizing the stick now at the end, now in the middle, and now near the crook. At length he seized the crook itself and with a wrench broke it off. A man who was passing . . . said, 'Clever dog that, sir; he knows where the hitch do lie.' The remark was the characteristic outcome of two minutes' chance observation" (507, pp. 142-143). How many anecdotes of animals are based on similar accidents?

It will be seen that in both the cases just criticised the error lies in the interpretation of the animal's behavior. Indeed, a root of evil in the method of anecdote consists in the fact that observation in this form is imperfectly divorced from interpretation. The maker of an anecdote

is seldom content with merely telling one what the animal did and leaving future investigation and the comparative study of many facts to decide what the animal's conscious experience in doing it was like. The point of the anecdote usually consists in showing that a human interpretation of the animal's behavior is possible. Here is shown the desire to tell a good story, which we mentioned among the pitfalls of the anecdotal method; the wish to report something unusual, not to get a just conception of the normal behavior of an animal. As Thorndike has forcibly put it: "Dogs get lost hundreds of times and no one ever notices it or sends an account of it to a scientific magazine. But let one find his way from Brooklyn to Yonkers and the fact immediately becomes a circulating anecdote. Thousands of cats on thousands of occasions sit helplessly yowling, and no one takes thought of it or writes to his friend the professor; but let one cat claw at the knob of a door supposedly as a signal to be let out, and straightway this cat becomes the representative of the cat-mind in all the books" (704, p. 4).

All this is not to deny that much of the testimony to be found in Romanes's "Animal Intelligence" and Darwin's "Descent of Man" is the trustworthy report of trained observers; but it is difficult to separate the grain from the chaff, and one feels toward many of the anecdotes the attitude of scepticism produced, for example, by this tale which an Australian lady reported to the Linnæan Society. The burial of some deceased comrades was accomplished, she says, by a nest of "soldier ants" near Sydney, in the following fashion. "All fell into rank walking regularly and slowly two by two, until they arrived at the spot where lay the dead bodies. . . . Two of the ants advanced and took up the dead body of one of their comrades; then

two others, and so on until all were ready to march. First walked two ants bearing a body, then two without a burden; then two others with another dead ant, and so on, until the line was extended to about forty pairs, and the procession now moved slowly onward, followed by an irregular body of about two hundred ants. Occasionally the two laden ants stopped, and laying down the dead ant, it was taken up by the two walking unburdened behind them, and thus, by occasionally relieving each other, they arrived at a sandy spot near the sea." A separate grave was then dug for each dead ant. "Some six or seven of the ants had attempted to run off without performing their share of the task of digging; these were caught and brought back, when they were at once attacked by the body of ants and killed upon the spot. A single grave was quickly dug and they were all dropped into it." No funeral procession for them! Of this story Romanes says, "The observation seems to have been one about which there could scarcely have been a mistake" (641, p. 91). One is inclined to think it just possible that there was.

§ 3. *Methods of Obtaining Facts: The Method of Experiment*

Diametrically opposed to the Method of Anecdote and its unscientific character is the Method of Experiment. An experiment, properly conducted, always implies that the conditions are controlled, or at least known; whereas ignorance of the conditions is, as we have seen, a common feature of anecdote. The experimenter is impartial; he has no desire to bring about any particular result. The teller of an anecdote wishes to prove animal intelligence. The experimenter is willing to report the facts precisely as he observes them, and is in no haste to make them prove

anything. The conduct of an experiment upon an animal will, of course, vary according to the problem to be solved. If the object is to test some innate reaction on the animal's part, such as its ordinary responses to stimulation or its instincts, one need merely place the animal under favorable conditions for observation, make sure that it is not frightened or in an abnormal state, supply the appropriate stimulus unmixed with others, and watch the result. If it is desired to study the process by which an animal learns to adapt itself to a new situation, one must, of course, make sure in addition that the situation really is new to the animal, and yet that it makes sufficient appeal to some instinctive tendency to supply a motive for the learning process.

As one might expect, among the earliest experiments upon animals were those made by physiologists with a view to determining the functions of sense organs. The experimental movement in psychology was slow in extending itself into the field of the animal mind.

Romanes, whose adherence to the anecdotal method we have noted, made in 1881, rather as a physiologist than as a psychologist, a number of exact and highly valued experiments on cœlenterates and echinoderms, which were summarized in his book entitled "*Jelly-fish, Star-fish, and Sea-urchins*," published in 1885. He has also recorded some rather informal experiments on the keenness of smell in dogs. Sir John Lubbock, in 1883, reported the results of some experiments on the color sense of the small crustacean *Daphnia*, and his book on "*Ants, Bees, and Wasps*," containing an account of experimental tests of the senses and "intelligence" of these insects, appeared in the same year. A German entomologist, Vitus Graber, experimented very extensively at about this period on the senses of sight and smell in many animals. Preyer, the authority on child

psychology, published in 1886 an experimental study of the behavior of the starfish. Loeb's work on the reactions of animals to stimulation began to appear in 1888. Max Verworn, the physiologist, published in 1889 an exhaustive experimental study of the behavior of single-celled animals. With the exception of Preyer and Romanes, all these men had but a secondary interest in comparative psychology: Bethe, indeed, as we shall see, wholly rejects it. Lloyd Morgan, who has written instructively on comparative psychology, makes but a limited use of the experimental method. Wesley Mills, professor of physiology in McGill University, has studied very carefully the mental development of young animals such as cats and dogs, but is inclined to criticise the use of experiment in observing animals. The work of E. L. Thorndike, whose "Animal Intelligence" appeared in 1898, represents, perhaps, the first definite effect of the modern experimental movement in psychology upon the study of the animal mind. Thorndike's aim in this research was to place his animals (chicks, cats, and dogs) under the most rigidly controlled experimental conditions. The cats and dogs, reduced by fasting to a state of "utter hunger," were placed in boxes, with food outside, and the process whereby they learned to work the various mechanisms which let them out was carefully observed. Since the appearance of Thorndike's work the performance of experiments upon animals has played much part in the work of psychological laboratories, particularly those of Harvard, Clark, and Chicago universities. The biologists and physiologists have continued their researches by this method, so that a very large amount of experimental work is now being done in comparative psychology.

Despite the obvious advantages of experiment as a method for the study of animal behavior, it is not without

its dangers. These were clearly stated by Wesley Mills in a criticism of Thorndike's "Animal Intelligence" (492). They may be summed up by saying that there is a risk of placing the animal experimented upon under abnormal conditions in the attempt to make them definite and controllable.¹ Did not, for example, the extreme hunger to which Thorndike's cats and dogs were reduced, while it simplified the conditions in one sense by making the strength of the motive to escape as nearly as possible equal for all the animals, complicate matters in another sense by diminishing their capacity to learn? Were the animals perhaps frightened and distracted by the unusual character of their surroundings? Thorndike thinks not (707); but whether or no he succeeded in averting these dangers, it is clear that they are real. It is also obvious that they are the more threatening, the higher the animal with which one has to deal. Fright, bewilderment, loneliness, are conditions more apt to be met with among the higher vertebrates than lower down in the scale, and the utmost care should be taken to make sure that animals likely to be affected by them are thoroughly trained and at home in their surroundings before the experimenter records results.

§ 4. *Methods of Obtaining Facts: The Ideal Method*

The ideal method for the study of a higher animal involves patient observation upon a specimen known from birth, watched in its ordinary behavior and environment, and occasionally experimented upon with proper control of the conditions and without frightening it or otherwise rendering it abnormal. The observer should acquaint himself with the individual peculiarities of each animal

¹ Cf. also Kline (402), and Vaschide and Rousseau (739).

studied, for there is no doubt that striking differences in mental capacity occur among the individuals of a single species. At the same time that he obtains the confidence of each individual animal, he should be able to hold in check the tendency to humanize it and to take a personal pleasure in its achievements if it be unusually endowed. This is, to say the least, not easy. Absolute indifference to the animals studied, if not so dangerous as doting affection, is yet to be avoided.

§ 5. *Methods of Interpreting Facts*

We may now turn from the problem of discovering the facts about animal behavior to the problem of interpreting them. If an animal behaves in a certain manner, what may we conclude the consciousness accompanying its behavior to be like? As we have seen, the interpretation is often confused with the observation, especially in the making of anecdotes; but theoretically the two problems are distinct. And at the outset of our discussion of the former, we are obliged to acknowledge that *all psychic interpretation of animal behavior must be on the analogy of human experience*. We do not know the meaning of such terms as perception, pleasure, fear, anger, visual sensation, etc., except as these processes form a part of the contents of our own minds. Whether we will or no, we must be anthropomorphic in the notions we form of what takes place in the mind of an animal. Accepting this fundamental proposition, the students of animals have yet differed widely in the conclusions they have drawn from it. Some have gone to the extreme of declaring that comparative psychology is therefore impossible. Others have joyfully hastened to make animals as human

as they could. Still others have occupied an intermediate position.

Descartes and Montaigne are the two writers antedating the modern period who are most frequently quoted in this connection. The latter had evidently a natural sympathy with animals. In that most delightful twelfth chapter of the second book of *Essays*, "An Apology of Raymond Sebonde," he gives free rein to the inclination to humanize them. I quote Florio's translation: "The Swallowes which at the approach of spring time we see to pry, to search and ferret all the corners of our houses; is it without judgment they seeke, or without discretion they chuse from out a thousand places, that which is fittest for them, to build their nests and lodging? . . . Would they (suppose you) first take water and then clay, unlesse they guessed that the hardnesse of the one is softned by the moistness of the other? . . . Why doth the spider spin her artificiall web thicke in one place and thin in another? And now useth one, and then another knot, except she had an imaginary kind of deliberation, forethought, and conclusion?" To ascribe such behavior to the working of mere instinct, "with a kinde of unknowne, naturall and servile inclination," is unreasonable. "The Fox, which the inhabitants of Thrace use" to test the ice on a river before crossing, which listens to the roaring of the water underneath and so judges whether the ice is safe or not; "might not we lawfully judge that the same discourse possesseth her head as in like case it would ours? And that it is a kinde of debating reason and consequence, drawne from natural sense? 'Whatsoever maketh a noyse moveth, whatsoever moveth, is not frozen. whatsoever is not frozen, is liquid; whatsoever is liquid, yeelds under any weight?'" (498).

Descartes, on the other hand, writing some sixty years later, takes, as is well known, the opposite ground. He says in a letter to the Marquis of Newcastle, "As for the understanding or thought attributed by Montaigne and others to brutes, I cannot hold their opinion." While animals surpass us in certain actions, it is, he holds, only in those "which are not directed by thought. . . . They act by force of nature and by springs, like a clock, which tells better what the hour is than our judgment can inform us. And doubtless when swallows come in the spring, they act in that like clocks. All that honey bees do is of the same nature" (183, pp. 281-283). The statement of Descartes, contained in the letter to Mersenne of July 30, 1640, that animals are automata, is often misunderstood. Descartes does not assert that animals are unconscious in the sense which that term would carry to-day, but only that they are without thought. Sensations, feelings, passions, he is willing to ascribe to them, in so far as these do not involve thought. "It must however be observed that I speak of thought, not of life, nor of sensation," he says in the letter to Henry More, 1649; "I do not refuse to them feeling . . . in so far as it depends only on the bodily organs" (183, p. 287). In this he does not go so far as some modern writers, who decline to assert the presence of any psychic process in the lower forms of animal life.

Turning to recent times, we find arguments very like those of Montaigne used by the earlier evolutionary writers. Darwin, for instance, says in "The Descent of Man," "As dogs, cats, horses, and probably all the higher animals, even birds, have vivid dreams, and this is shown by their movements and the sounds uttered, we must admit that they possess some power of imagination" (169, p. 74). "Even

brute beasts," says Montaigne, ". . . are seen to be subject to the power of imagination; witnesse some Dogs . . . whom we ordinarily see to startle and barke in their sleep" (501, Bk. I, ch. 20). "Only a few persons," Darwin continues, "now dispute that animals possess some power of reasoning. Animals may constantly be seen to pause, deliberate, and resolve." And he states that his object in the third chapter of the work quoted is "to show that there is no fundamental difference between man and the higher mammals in their mental faculties" (169, p. 66). Romanes is evidently guided by the same desire to humanize animals.

Now these writers were not led to take such an attitude merely out of general sympathy with the brute creation, like Montaigne; they had an ulterior motive; namely, to meet the objection raised in their time against the doctrine of evolution, based on the supposed fact of a great mental and moral gulf between man and the lower animals. They wished to show, as Darwin clearly states, that this gulf is not absolute but may conceivably have been bridged by intermediate stages of mental and moral development. While this argument against evolution was being pressed, the evolutionary writers were very unsafe guides in the field of animal psychology, for they distinctly "held a brief for animal intelligence," to use Thorndike's phrase. In more recent times interest in both the positive and the negative sides of the objection drawn from man's superiority has died out, and such special pleading has become unnecessary.

On the other hand, the fact that the greater part of the experiments on animals were until the last ten or fifteen years performed by physiologists has given rise to an opposite tendency in interpreting the animal mind: the

tendency to make purely biological concepts suffice as far as possible for the explanation of animal behavior and to assume the presence even of consciousness in animals only when it is absolutely necessary to do so. Loeb in 1890 suggested the theory which he has since elaborated, that the responses of animals to stimulation, instead of being signs of "sensation," are in every way analogous to the reactions of plants to such forces as light and gravity; hence unconscious "tropisms" (421). Bethe in 1898 attempted to explain all the complicated behavior of ants and bees, which the humanizing writers had compared with our own civilization, as a result of reflex responses, chiefly to chemical stimulation, unaccompanied by any consciousness whatever (51). This revival, in an altered form, of the Cartesian doctrine has met with energetic opposition, especially from writers having philosophical interests. When the first edition of the present work appeared, the parties in the controversy could be divided into three groups: those who believed that consciousness should be ascribed to all animals; those who believed that it should be ascribed only to those animals whose behavior presents certain peculiarities regarded as evidence of mind; and those who held that we have no trustworthy evidence of mind in any animal, and should therefore abandon comparative psychology and use only physiological terms. Of recent years, the tendency has been towards the survival only of the two extreme parties: it has been more and more recognized that there exists no evidence of mind which is not either equally bad or equally good in the case of all animals.

Among the authorities who would ascribe mind to all animals belong Claparède of Geneva, the Swiss naturalist Forel, and the Jesuit Wasmann. They maintain

this position from widely different philosophical points of view. The first-named is what is called a parallelist; that is, he believes that mental processes and bodily processes are not causally related, but form two parallel and non-interfering series of events. In the study of animals, both the physical and the psychical series should, he thinks, be investigated. Biology should use two parallel methods, the **one** ascending, attempting to explain animal behavior by physical and chemical laws; the other descending, giving an account of the mental processes of animals. Ultimately, it may be hoped, according to Claparède, that both methods will be applied throughout the whole range of animal life. At present the ascending method is most successful with the lowest forms, the descending method with the highest forms. We cannot afford to abandon the psychological study of animals, for our knowledge of the nervous processes underlying the higher mental activities is very slight; physiology here fails us, and psychology must be left in command of the field. The danger besetting the attempt at a purely physical explanation of animal behavior is that the facts shall be unduly simplified to fit the theory. Thus Bethe's effort at explaining the way in which bees find their way back to the hive as a reflex response, or tropism, produced by "an unknown force," is highly questionable; the facts seem to point toward the exercise of some sort of memory by the bees. It is always possible, further, that the tropism is accompanied by consciousness. A physiologist from Saturn might reduce all human activities to tropisms, says Claparède in a striking passage. "The youth who feels himself drawn to medical studies, or he who is attracted to botany, can no more account for his profoundest aspirations than the beetle which runs to the odor of a dead animal or the butterfly invited by the flowers; and if the

first shows a certain feeling corresponding to these secret states of the organism (a feeling of 'predilection' for such a career, etc.), how can we dare to deny to the second analogous states of consciousness?" (122). If it is argued that we have no direct, but only an inferential, knowledge of the processes in an animal's mind, the argument is equally valid against human psychology, for the psychologist has only an inferential knowledge of his neighbor's mind (124).

Wasmann defends the animal mind from a different position. For one thing, he believes that mental processes may act causally upon bodily states. He accepts, in other words, what is called interactionism, as opposed to parallelism. Further, although he strongly opposes the doctrine that the reactions of animals are unconscious tropisms and constantly emphasizes their variability and modifiability through experience, he nevertheless believes that a gulf separates the human from the animal mind. The term "intelligence" which most writers use to designate merely the power of learning by individual experience, Wasmann would reserve for the power of deducing and understanding relations, and would assign only to human beings (761, 762). Although animals have their instincts modified by sense experience, man "stands through his reason and freedom immeasurably high above the irrational animal that follows, and must follow, its sensuous impulse without deliberation" (763).

Forel, in the third place, is what is called a monist in metaphysics. That is, he does not believe either that mind and body are parallel, or that they interact causally, but that they are two aspects of the same reality. "Every psychic phenomenon is the same real thing as the molecular or neurocymic activity of the brain-cortex coinciding with

it" (233, p. 7). The psychic and the physical, on this theory, should be coextensive; not merely should consciousness in some form belong to all living things, but every atom of matter should have its psychic aspect. On such a basis, Forel takes highly optimistic views of the animal mind. In insects, of which he has made a special study, it is, he thinks, "possible to demonstrate the existence of memory, associations of sensory images, perceptions, attention, habits, simple powers of inference from analogy, the utilization of individual experience, and hence distinct, though feeble, plastic individual deliberations or adaptations" (233, p. 36).

A peculiar position on the problem of mind in animals is occupied by the "vitalists," of whom Driesch (191) is the foremost representative. They regard the reactions of organisms as requiring the operation of psychic forces or "entelechies"; they hold that as physical phenomena such reactions cannot be explained save through the working of these psychic forces. A living being is forever distinguished from a lifeless creature by the presence of such entelechies. Thus the vitalist is an interactionist and a dualist: the worlds of the lifeless and the living are to him forever distinct.

The opposite camp is represented by Bethe, Beer, von Uexküll, Loeb, and other physiologists, as well as by Watson.

The eminent neurologist Bethe, in his study of the behavior of ants and bees, refuses to allow these animals any "psychic qualities" whatever, and suggests the term "chemo-reception" instead of "smell," to designate the influence which directs most of their reactions, — "smell" implying a psychic quality (51). In a footnote to a later article he says: "Psychic qualities cannot be demonstrated.

Even what we call sensation is known to each man only in himself, since it is something subjective. We possess the capacity of modifying our behavior [*i.e.* of learning], and every one knows from his own experience that psychic qualities play a part connected with this modifying process. Every statement that another being possesses psychic qualities is a conclusion from analogy, not a certainty; it is a matter of faith. If one wishes to draw this analogical inference, it should be made where the capacity for modification can be shown. When this is lacking, there is not the slightest scientific justification for assuming psychic qualities. They *may* exist, but there is no probability of it, and hence science should deny them. Hence if one ventures to speak of a Psych in animals at all, one should give the preference to those which can modify their behavior" (51). But that Bethe himself prefers not to make the venture is evident from statements in the text of the same article. The psychic or subjective, he says, is unknowable, and the only thing we may hope to know anything about is the chemical and physiological processes involved. "These chemo-physical processes and their consequences, that is, the objective aspect of psychic phenomena, and these alone, should be the object of scientific investigation" (51).

Together with Beer and von Uexküll, Bethe shortly afterward published "Proposals for an Objectifying Nomenclature in the Physiology of the Nervous System." The main purpose of this paper was to suggest that all terms having a psychological implication, such as sight, smell, sense-organ, memory, learning, and the like, be carefully excluded from discussions of animal reactions to stimulation and animal behavior generally. In their stead the authors propose such expressions as the following: for

responses to stimulation where no nervous system exists, the term *antitypes*; for those involving a nervous system, *antikineses*; the latter are divided into *reflexes*, where the response is uniform, and *antiklises*, where the response is modifiable. A sense-organ becomes a *reception-organ*, sensory nerves are *receptory-nerves*, and we have *phono-reception*, *stibo-reception*, *photo-reception*, instead of hearing, smell, and sight. The after-effect of a stimulus upon later ones is the *resonance* of the stimulus (39).

Loeb (434) agrees with Bethe that physico-chemical processes and not states of consciousness are the proper objects of investigation for the "psychologist." These men evidently regard the universe as essentially uniform throughout — there exists for them no gulf between living and lifeless things; the behavior of living beings will be reduced to a series of chemical reactions as soon as science has progressed sufficiently far. They are "mechanists." It is, however, perfectly possible to be a mechanist so far as the explanation of animal behavior is concerned, and still admit that animals have consciousness and that their behavior is accompanied by inner, mental states which it is the business of the psychologist to investigate. One does not have to be a vitalist to believe that animals have minds: one may hold that every action of an animal will some day be explained as the result of physico-chemical processes, and yet maintain that the actions of animals are conscious. The consciousness would be an accompaniment, an inner aspect, of the physico-chemical processes.

The views of Loeb and Bethe have gained much ground lately among certain American psychologists, notably Watson (771). The position of these "behaviorists" seems not to have been fully thought out in its philosophical aspects, but is somewhat as follows. The difficulties of

interpreting an animal's mind from its behavior are so great that such inferences have no scientific value. We may therefore proceed as if animals had no minds; or rather, as if mind were a kind of behavior, observable by outside means. Since it is obvious that the difficulty of interpreting an animal's mind from its behavior is only greater in degree than, not unlike in kind, the difficulty of interpreting other human minds from behavior, human psychology also should confine itself to the observation merely of the actions of other persons, and permit no inferences as to the inner aspect of such actions. In fact, there is no inner aspect to such actions—thoughts and feelings, human as well as animal, are only behavior, and if we have at present no instruments for inspecting and measuring the movements which are thoughts and feelings, such instruments will in time be discovered.

In opposition to these views, we shall in this book maintain the following position. There exists an inner aspect to behavior, the realm of sensations, feelings, and thoughts, which is not itself identical with behavior or with any form of movement. Thoughts probably always have as their accompaniment bodily movements, but the thought is not identical with the movement. If a physiologist perfected an instrument by which he could observe the nervous process in my cortex that occurs when I am conscious of the sensation red, he would see nothing red about it; if he could watch the bodily movements that result from this stimulation, say, for instance, the slight contraction of the articulatory muscles that occurs when I say "red" to myself, he would not see them as red. The red is in my consciousness, and no devices for observing and registering my movements will ever observe the red, though they may easily lead to the inference that it exists in my con-

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sciousness.' And precisely the same is true of all my sensations, thoughts, and feelings.

Since an inner world of experience exists, we may legitimately try to investigate it. For this purpose we possess a method, which is called introspection. We can, that is, attentively and, if we have had practice, dispassionately and scientifically, observe what goes on in our own consciousness when we receive certain stimuli and make certain movements. Further, we can, by the use of the same kind of inference from one case to another similar case, upon which all scientific generalization is based, infer that when a being whose structure resembles ours receives the same stimulus that affects us and moves in the same way as a result, he has an inner experience which resembles our own. Finally, we may extend this inference to the lower animals, with proper safeguards, just as far as they present resemblances in structure and behavior to ourselves. Our object in this book will always be the interpretation of the inner aspect of the behavior of animals; we shall be interested in what animals do only as it throws light upon what they feel. To the true psychologist, no challenge is so enticing as that presented by the problem of how it feels to be another person or another animal; and although we must sometimes give up the problem in despair, yet we have also our successes. We have wonderfully advanced, within the last twenty-five years, in knowledge as to how the world looks from the point of view of our brother animals.

We may now note briefly some of the special precautions that must be observed in interpreting the conscious aspect of animal behavior. First, there is no doubt that great caution should be used in regarding the quality of a human conscious process as identical with the quality

of the corresponding process in the animal mind. For example, we might say with a fair degree of assurance that an animal consciously discriminates between light and darkness; that is, receives conscious impressions of different quality from the two, yet the mental impression produced by white light upon the animal may be very different from the sensation of white as we know it, and the impression produced by the absence of light very different from our sensation of black. Black and white may, for all we know, depend for their quality upon some substance existing only in the human retina.

A second precaution concerns the simplicity or complexity of the interpretation put upon animal behavior. Lloyd Morgan, in his "Introduction to Comparative Psychology," formulated a conservative principle of interpretation which has often been quoted as "Lloyd Morgan's Canon." The principle is as follows: "In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale" (505, p. 53). In other words, when in doubt take the simpler interpretation. For example, a dog detected in a theft cowers and whines. One possible mental accompaniment of this behavior is remorse; the dog is conscious that he has fallen below a moral standard, and grieved or offended his master. A second is the anticipation of punishment; the dog has a mental representation of the consequences of his action upon former occasions, and imagining himself likely to experience them anew, is terrified at the prospect. A third possibility is that the dog's previous experience of punishment, instead of being revived in the form of definite images, makes itself effective merely in his feelings and behavior; he is uncomfortable and fright-

ened, he knows not definitely why. It is evident that these three possibilities represent three different grades of complexity of mental process, the first being by far the highest. Lloyd Morgan's canon enjoins upon us in such a case to prefer the third alternative, provided that it will really account for the dog's behavior.

Now why should the simplest interpretation be preferred? We must not forget that the more complex ones remain in the field of possibility. Dogmatic assertions have no place in comparative psychology. We cannot say that the simplicity of an hypothesis is sufficient warrant of its truth, for nature does not always proceed by the paths which seem to us least complicated. The fact is that Lloyd Morgan's principle serves to counterbalance our most important source of error in interpreting animal behavior. It is like tipping a boat in one direction to compensate for the fact that some one is pulling the opposite gunwale. We must interpret the animal mind humanly if we are to interpret it at all. Yet we know that it differs from the human mind, and that the difference is partly a matter of complexity. Let us therefore take the least complex interpretation that the facts of animal behavior will admit, always remembering that we may be wrong in so doing, but resting assured that we are, upon the whole, on the safer side. The social consciousness of man is very strong, and his tendency to think of other creatures, even of inanimate nature, as sharing his own thoughts and feelings, has shown itself in his past to be almost irresistible. Lloyd Morgan's canon offers the best safeguard against this natural inclination, short of abandoning all attempt to study the mental life of the lower animals.

CHAPTER II

THE EVIDENCE OF MIND

§ 6. *Inferring Mind from Behavior*

IN this chapter we shall try to show that there exists no evidence for denying mind to any animals, if we do not deny it to all; in other words, that there is no such thing as an objective proof of the presence of mind, whose absence may be regarded as proof of the absence of mind.

To begin with, can it be said that when an animal makes a movement in response to a certain stimulus, there is an accompanying consciousness of the stimulus, and that when it fails to move, there is no consciousness? Is *response to stimulation* evidence of consciousness? In the case of man, we know that absence of visible response does not prove that the stimulus has not been sensed; while it is probable that some effect upon motor channels always occurs when consciousness accompanies stimulation, the effect may not be apparent to an outside observer. On the other hand, if movement in response to the impact of a physical force is evidence of consciousness, then the ball which falls under the influence of gravity and rebounds on striking the floor is conscious. Nor is the case improved if we point out that the movements which animals make in response to stimulation are not the equivalent in energy of the stimulus applied, but involve the setting free of energy stored in the animal as well. True, when a microscopic animal meets an obstacle in its swimming, and darts backward, the movement is

not a mere rebound; it implies energy contributed by the animal's own body. But just so an explosion of gunpowder is not the equivalent in energy of the heat of the match, the stimulus. Similarly it is possible to think of the response made by animals to external stimuli as involving nothing more than certain physical and chemical processes identical with those existing in inanimate nature.

If we find that the movements made by an animal as a result of external stimulation regularly involve withdrawal from certain stimuli and acceptance of others, it is natural to use the term "*choice*" in describing such behavior. But if consciousness is supposed to accompany the exercise of choice in this sense, then consciousness must be assumed to accompany the behavior of atoms in chemical combinations. When hydrochloric acid is added to a solution of silver nitrate, the atoms of chlorine and those of silver find each other by an unerring "*instinct*" and combine into the white precipitate of silver chloride, while the hydrogen and the nitric acid similarly "*choose*" each other. Nor can the fact that behavior in animals is adapted to an end be used as evidence of mind; for "*purposive*" reactions, which contribute to the welfare of an organism, are themselves selective. The search for food, the care for the young, and the complex activities which further welfare, are made up of reactions involving "*choice*" between stimuli; and if the simple "*choice*" reaction is on a par with the behavior of chemical atoms, so far as proof of consciousness goes, then *adaptation to an end*, apparent purposiveness, is in a similar position.

Thus the mere fact that an animal reacts to stimulation, even selectively and for its own best interests, offers no evidence for the existence of mind that does not apply equally well to particles of inanimate matter. Moreover, there is

some ground for holding that the reactions of the lowest animals are unconscious. This ground consists in the apparent lack of variability which characterizes such reactions. In our own case, we know that certain bodily movements, those of digestion and circulation, for example, are normally carried on without accompanying consciousness, and that in other cases where there is consciousness of the stimulus, as in the reflex knee-jerk, it occurs after the movement is initiated, so that the nervous process underlying the sensation would seem to be immaterial to the performance of the movement. These unconscious reactions in human beings are characterized by their relative uniformity, by the absence of variation in their performance. Moreover, when an action originally accompanied by consciousness is often repeated, it tends, by what is apparently one and the same process, to become unconscious and to become uniform. There is consequently reason for believing that when the behavior of lower animals displays perfect uniformity, consciousness is not present. On the other hand, an important reservation must be made in the use of this negative test. It is by no means easy to be sure that an animal's reactions are uniform. The more carefully the complexer ones are studied, the more are variability and difference brought to light where superficial observation had revealed a mechanical and automatic regularity. It is quite possible that even in the simple, apparently fixed response of microscopic animals to stimulation, better facilities for observation might show variations that do not now appear.

This matter of uniformity *versus* variability suggests a further step in our search for a satisfactory test of the presence of mind. Is mere *variability* in behavior, mere irregularity in response, to be taken as such a test? Not if

we argue from our own experience. While that portion of our own behavior which involves consciousness shows more irregularity than the portion which does not, yet the causes of the irregularity are often clearly to be found in physiological conditions with which consciousness has nothing to do. There are days when we can think clearly and recall easily, and days when obscurities refuse to vanish and the right word refuses to come; days when we are irritable and days when we are sluggish. Yet since we can find nothing in our mental processes to account for this variability, it would be absurd to take analogous fluctuations in animal behavior as evidence of mind. So complicated a machine as an animal organism, even if it be nothing more than a machine, must show irregularities in its working.

Behavior, then, must be variable, but not merely variable, to give evidence of mind. The criterion most frequently applied to determine the presence or absence of the psychic is *a variation in behavior that shows definitely the result of previous individual experience*. "Does the organism," says Romanes, "learn to make new adjustments, or to modify old ones, in accordance with the results of its own individual experience?" (641, p. 4). Loeb declared that "the fundamental process which occurs in all psychic phenomena as the elemental component" is "the activity of the associative memory, or of association," and defines associative memory as "that mechanism by which a stimulus brings about not only the effects which its nature and the specific structure of the irritable organ call for, but by which it brings about also the effects of other stimuli which formerly acted upon the organism almost or quite simultaneously with the stimulus in question." "If an animal can be trained," he continued, "if it can learn, it possesses

associative memory," and therefore mind (429, p. 12). The psychologist finds the term "associative memory" hardly satisfactory, and objects to the confusion between mental and physical concepts which renders it possible to speak of a "mechanism" as forming an "elemental component" in "psychic phenomena," but these points may be passed over. The power to learn by individual experience is the evidence which Romanes, Morgan, and Loeb will accept as demonstrating the presence of mind in an animal.

Does the absence of proof that an animal learns by experience show that the animal is unconscious? Romanes is careful to answer this question in the negative. "Because a lowly organized animal," he says, "does *not* learn by its own individual experience, we may not therefore conclude that in performing its natural or ancestral adaptations to appropriate stimuli, consciousness, or the mind element, is wholly absent; we can only say that this element, if present, reveals no evidence of the fact" (641, p. 3). Loeb, on the other hand, wrote as if absence of proof for consciousness amounted to disproof, evidently relying on the principle of parsimony, that no unnecessary assumptions should be admitted. "Our criterion," he remarked, "puts an end to the metaphysical ideas that all matter, and hence the whole animal world, possesses consciousness" (429, p. 13). If learning by experience be really a satisfactory proof of mind, then its absence in certain animals would indeed prevent the positive assertion that all animals are conscious; but it could not abolish the possibility that they might be. Such a possibility might, however, be of no more scientific interest than any one of a million wild possibilities that science cannot spare time to disprove. But we shall find that learning by experience, taken by itself, is too indefinite a concept to be of much service, and

that when defined, it is inadequate to bear the whole weight of proving consciousness in animals. Such being the case, the possibility that animals which have not been shown to learn may yet be conscious acquires the right to be reckoned with.

The first point that strikes us in examining the proposed test is that the learning by experience must not be too slow, or we can find parallels for it in the inanimate world. An animal may be said to have learned by experience if it behaves differently to a stimulus because of preceding stimuli. But it is one thing to have behavior altered by a single preceding stimulus, and another to have it altered by two hundred repetitions of a stimulus. The wood of a violin reacts differently to the vibrations of the strings after it has "experienced" them for ten years; the molecules of the wood have gradually taken on an altered arrangement. A steel rail reacts differently to the pounding of wheels after that process has been long continued; it may snap under the strain. Shall we say that the violin and the rail have learned by individual experience? If the obvious retort be made that it is only in living creatures that learning by experience should be taken as evidence of mind, let us take an example from living creatures. When a blacksmith has been practising his trade for a year, the reactions of his muscles are different from what they were at the outset. But this difference is not merely a matter of more accurate sense-discrimination, a better "placing" of attention and the like; there have been going on within the structure of his muscles changes which have increased their efficiency, and with which consciousness has had nothing to do. These changes have been extremely slow compared to the learning which does involve consciousness. In one or two lessons the apprentice learned what he was to do; but only

very gradually have his muscles acquired the strength to do it as it should be done. Now among the lower animal forms we sometimes meet with learning by experience that is very slow; that requires a hundred or more repetitions of the stimulus before the new reaction is acquired. In such a case we can find analogical reasons for suspecting that a gradual change in the tissues of the body has taken place, of the sort which, like the attuning of the violin wood or the slow development of a muscle, have no conscious accompaniment.

We must then ask the question: *What kind of learning by experience never, so far as we know, occurs unconsciously?* Suppose a human being shut up in a room from which he can escape only by working a combination lock. As we shall see later, this is one of the methods by which the learning power of animals has been tested. The man, after prolonged investigation, hits upon the right combination and gets out. Suppose that he later finds himself again in the same predicament, and that without hesitation or fumbling he opens the lock at once, and performs the feat again and again, to show that it was not a lucky accident. But one interpretation of such behavior is possible. We know from our own experience that the man could not have worked the lock the second time he saw it, unless he consciously remembered the movements he made the first time; that is, unless he had in mind some kind of idea as a guide. Here, at least, there can have been no change in the structure of the muscles, for such changes are gradual; the change must have taken place in the most easily alterable portion of the organism, the nervous system; and further, it must have taken place in the most unstable and variable part of the nervous system, the higher cortical centres whose activity is accompanied by consciousness. In other words, we may be practically

assured that consciousness accompanies learning only when the learning is so rapid as to show that the effects of previous experience are recalled in the guise of an idea or mental image of some sort. But does even the most rapid learning possible assure us of the presence of an idea in the mind of a lower animal? Where the motive, the beneficial or harmful consequence of action, is very strong, may not a single experience suffice to modify action without being revived in idea? Moreover, animals as high in the scale as dogs and cats learn to solve problems analogous to that of the combination lock so slowly that we cannot infer the presence of ideas. Are we then to conclude that these animals are unconscious, or that there is absolutely no reason for supposing them possessed of consciousness? Yerkes has criticised the "learning by experience" criterion by pointing out that "no organism . . . has thus far been proved incapable of profiting by experience." It is a question rather of the rapidity and of the kind of learning involved. "The fact that the crayfish need a hundred or more experiences for the learning of a type of reaction that the frog would learn with twenty experiences, the dog with five, say, and the human subject with perhaps a single experience, is indicative of the fundamental difficulty in the use of this sign" (814). Nagel has pointed out that Loeb, in asserting "associative memory" as the criterion of consciousness, offers no evidence for his statement (524). The fact is that while proof of the existence of mind can be derived from animal learning by experience only if the learning is very rapid, other evidence, equally valid on the principle of analogy, makes it *highly improbable that all animals which learn too slowly to evince the presence of ideas are therefore unconscious*. This evidence is of a *morphological* character.

§ 7. *Inferring Mind from Structure*

Both Yerkes and Lukas urge that the resemblance of an animal's nervous system and sense organs to those of human beings ought to be taken into consideration in deciding whether the animal is conscious or not. Lukas suggests that the criteria of consciousness should be grouped under three heads: morphological, including the structure of the brain and sense-organs, physiological, and teleological. Under the second rubric he maintains that "individual purposiveness" is characteristic of the movements from which consciousness may be inferred; that individual purposiveness pertains only to voluntary acts, and that voluntary acts and acts "which are preceded by the intention to perform a definite movement, hence by the idea of this movement." We have reached the same conclusion in the preceding paragraph. The third test of the presence of consciousness, the teleological test, rests on the consideration: "What significance for the organism may be possessed by the production of a conscious effect by certain stimuli?" (445). This test, however, being of a purely *a priori* character, would seem to be distinctly less valuable than the others.

Yerkes proposes "the following six criteria in what seems to me in general the order of increasing importance. The functional signs are of greater value as a rule than the structural; and within each of the categories the particular sign is usually of more value than the general. In certain cases, however, it might be maintained that neural specialization is of greater importance than modifiability.

I. Structural Criteria.

1. General form of organism (Organization).

2. Nervous system (Neural organization).
3. Specialization in the nervous system (Neural specialization).

II. Functional Criteria.

1. General form of reaction (Discrimination).
2. Modifiability of reaction (Docility).
3. Variability of reaction (Initiative)" (814).

The terms "discrimination," "docility," and "initiative" in this connection are borrowed from Royce's "Outlines of Psychology" (649).

If resemblance of nervous and sense-organ structure to the human type is to be taken along with rapid learning as co-ordinate evidence of consciousness, it is clear that here also we have to deal with a matter of degree. The structure of the lower animals differs increasingly from our own as we go down the scale. At what degree of difference shall we draw the line and say that the animals above it may be conscious, but that those below it cannot be? No one could possibly establish such a line. The truth of the whole matter seems to be this: *We can say neither what amount of resemblance in structure to human beings, nor what speed of learning, constitutes a definite mark distinguishing animals with minds from those without minds, unless we are prepared to assert that only animals which learn so fast that they must have memory ideas possess mind at all.* And this would conflict with the argument from structure. For example, there is no good experimental evidence that cats possess ideas, yet there is enough analogy between their nervous systems and our own to make it improbable that consciousness, so complex and highly developed in us, is in them wholly lacking. We know not where consciousness begins in the animal world. We know where it surely resides — in ourselves; we know where it exists beyond a reason-

able doubt—in those animals of structure resembling ours which rapidly adapt themselves to the lessons of experience. Beyond this point, for all we know, it may exist in simpler and simpler forms until we reach the very lowest of living beings.

CHAPTER III

THE MIND OF THE SIMPLEST ANIMALS

§ 8. *The Structure and Behavior of Amœba*

WE have seen in the last chapter that no one can prove the absence of consciousness in even the simplest forms of living beings. It is therefore perfectly allowable to speculate as to what may be the nature of such consciousness, provided that the primitive organisms concerned possess it. Perfectly allowable, yet also perfectly useless, many authorities would argue; the remoteness of the creatures from ourselves in structure and behavior renders theorizing about their conscious experience, which is probably non-existent and certainly unimaginable in any definite terms by us, the idlest form of mental exercise.

Undeniably the formation of a positive notion regarding the character and content of psychic states in the mind, say of an Amœba, is next door to an impossibility. Yet it may not be wholly a waste of time if we spend a few pages in the attempt to discover *wherein the simplest type of mind, supposing it to be that belonging to the simplest type of animal, necessarily differs from our own*. Some light, perhaps, may be cast upon the growth of mental life in complexity if we try to make clear to ourselves what primitive consciousness is not, though we may not be able to find in our own experience any elements that shall properly represent what it is.

The first need is evidently information about the structure and the behavior of a primitive animal. For this purpose

the *Amœba* presents itself as a good subject. Structurally, it consists of a single cell, as do all the Protozoa, the lowest group of animals; it is so small that it can be studied only through the microscope; its form, at least that of *Amœba proteus*, the most typical species, is irregular and constantly changing in locomotion or in response to stimulation. While the internal substance of its body shows a certain amount of differentiation, there is no trace whatever of special modifications that might be supposed to serve for the conduction of stimuli to different parts of the body, and thus represent the prototype of a nervous system. Nor have any structures been found that could conceivably be used for the special reception of stimuli; that is, there are no sense organs. So far as the anatomy of the animal is concerned, then, it differs so widely from our own that we could only conclude from it the absence of all those features which our conscious experience involves.

Turning from structure to behavior, we find the external activities of *Amœba*, that is, those not confined to the inner processes of its cell body, to be superficially, at least, divisible into two classes: movements of locomotion and responses to stimulation. *Amœba*, though a water-dwelling animal, is not a free-swimming one, but moves by crawling on a solid body. This method of locomotion involves in *Amœba proteus* changes of form on the animal's part, projections, called pseudopodia, being sent out in advance of the movement of the whole body. The protoplasm of the body shows in this process certain flowing movements which are differently described by different observers, and doubtless vary in different species: thus Rhumbler finds that the protoplasmic currents move backward along the sides of the animal and forward through the middle in a way quite comparable to the behavior of currents in a drop of any

fluid where the tension of the surface is diminished in front, *i.e.*, at the point toward which the drop, in consequence of the diminished tension there, rolls. Such movements, Rhumbler shows, can be reproduced by placing, say, a drop of clove oil under the proper conditions of surface tension (632, 633). Jennings, on the other hand, has observed, at least in certain species of *Amœba*, that the protoplasmic currents are all forward in direction, the movement being really one of rolling, complicated by the attachment of the lower part of the body to the solid object on which the animal crawls. Mechanical conditions of surface tension would not account for such currents (371, 373, 378). Dellinger rejects both the surface tension and the "rolling" theories, and from a study of side views of the moving *Amœba* concludes that progression occurs through the advancement of the front end freely through the water and its subsequent attachment, the rest of the body following through active contraction brought about by a contractile substance (181). The problem is of great interest to the student of vital phenomena, but its bearing on the question of mind in the *Amœba* is so obscure that we need not consider it further, but may pass at once to the study of the animal's reactions to special stimulation.

These are, according to Jennings (373, 378), the foremost authority on the behavior of the lowest organisms, three in number; namely, the negative, the positive, and the food-taking reactions. First, if an *Amœba* comes into strong contact with a solid obstacle in its movements, or if a solution of different composition from the water in which it lives strikes against it, or if one side of it is heated, the animal responds by contracting the part stimulated, releasing it from the substratum, and moving in another direction, usually one forming only a small angle with the

preceding one. If the whole of one side or end receives a strong stimulus, if light falls on one side, or an electric current is passed through the water, the side stimulated — in the case of the electric current, the side toward the positive pole — contracts as a whole, and the movement takes place in the opposite direction. These phenomena constitute the *negative* reaction (Fig. 1).

Secondly, the reaction to solid bodies sometimes takes a *positive* form. In this case a pseudopodium is pushed forward in the direction of the stimulus, and the animal moves toward the solid. As the negative reaction serves the purpose of avoiding obstacles, so the positive reaction is useful in securing contact with a support on which to creep, and with food. It seems to be given in response to weak mechanical stimuli, stronger ones producing the negative reaction. No chemicals have been found to occasion it, but weak chemical stimulation very likely coöperates with mechanical stimulation when the positive reaction is given to food.

Schaeffer (659) has recently obtained evidence that *Amœba* can give the positive reaction to insoluble and inedible objects before they come into contact with it. The way in which such objects can act as stimuli is still unexplained. It is possible that the movement of the *Amœba* produces water currents which are reflected

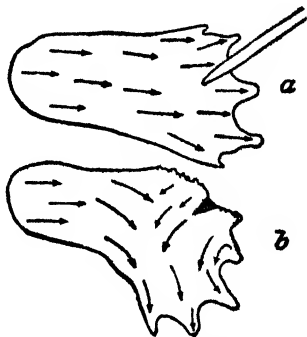


FIG. 1. — Negative reaction of *Amœba* to stimulation by a glass rod. *a*. Application of the stimulus. *b*. Change of direction of movement. After Jennings (378).

back in a peculiar way by such particles. He reports also (660) that the positive reaction is given to beams of light which pass no nearer than 100-150 thousandths of an inch to the animal. The *Amœba* moves towards the beam, but when it comes into contact with it, the movement ceases, and in some cases a negative response occurs.

Thirdly, there is the *food-taking reaction*. This consists for *Amœba proteus*, according to Jennings, in the pushing forward of a pseudopodium on either side of the particle of

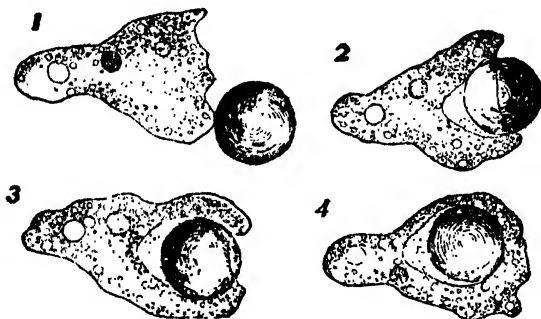


FIG. 2. — Food-taking reaction of *Amœba*. 1, 2, 3, 4, successive stages.
After Jennings (378).

food that has come into contact with the animal; the bending over of the ends of the pseudopodia so as to grasp the food, while "a thin sheet of protoplasm" spreads from the upper surface of the animal over it; and the final fusion of the ends of the pseudopodia and the ends of this sheet, so as to take the food directly into the animal's body. The reaction may occur anywhere on the body surface, there being no specialized mouth. It appears to be made only in response to edible substances, hence there is doubtless some chemical peculiarity about the stimulus which makes it effective (378).

Kepner and Taliaferro (399) find the food-taking reaction

more complex and variable than Jennings's account describes it to be. They observed cases where only one pseudopodium was formed, and cases where it was put forth not at the exact point acted upon by the stimulus. The nature of the reaction varied in such a way as to prevent the "swallowing" of too much water along with the food: "the parts that could most advantageously respond did so." McClendon (451 a) has attempted to apply the surface tension theory to the positive, negative, and feeding reactions of *Amœba*, suggesting that the stimuli may exert an electric influence whereby the surface tension at the point stimulated becomes less in the case of the positive reactions and feeding, greater in the negative reaction. But such variations as those just described are difficult to reconcile with a surface tension theory. Moreover Mast and Root (477) have observed *Amœba* crushing its prey with a force far greater than surface tension could account for. Schaeffer (658) suggests that a chemical discrimination may occur inside the *Amœba* after substances have been taken in, for, he says, when carmine grains have been swallowed, the *Amœba* at once begins to move off in such a way as to bring the grains to the hinder part of the body where they will be ejected. "The carmine grains are ejected . . . because they are actually disagreeable and not merely because they are (presumably) indigestible." A hungry *Amœba*, when it comes within 100 thousandths of an inch from an organism, which is as a whole at rest but moving certain portions of its body, will begin to move towards it and to form a food cup before actual contact occurs. Probably the slight water currents produced by the movements of the prey act as the stimulus in this case. Any stimulus which proceeds from a moving object tends, as we shall see, to be peculiarly effective.

These three reactions make up, together with the ordinary crawling locomotion, the variety of the Amœba's experience as displayed in behavior, with the addition of a peculiar set of movements occurring in the *absence of all mechanical stimulation*. When an Amœba is floating in the water, through some chance, unattached to any solid, "such a condition," says Jennings, "is most unfavorable for its normal activities; it cannot move from place to place, and has no opportunity to obtain food." Its mode of getting out of the difficulty is to send out "long, slender pseudopodia in all directions," until "the body may become reduced to little more than a meeting point for these pseudopodia" (378, p. 8). As soon as one of these "feelers" comes in contact with a solid, it attaches itself, and the whole animal following soon takes up its normal crawling locomotion.

§ 9. *The Mind of Amœba*

Now what light does the behavior of Amœba throw upon the nature of the animal's possible consciousness? The first thought which strikes us in this connection is that *the number of different sensations occurring in an Amœba's mind, if it has one, is very much smaller than the number forming the constituent elements of our own experience*. We human beings have the power to discriminate several thousand different qualities of color, brightness, tone, noise, temperature, pressure, pain, smell, taste, and other sensation classes. Thus the content of our consciousness is capable of a great deal of variety. It is hard to see how more than three or four qualitatively different processes can enter into the conscious experience of an Amœba. The negative reaction is given to all forms of strong stimulation alike, with the single exception of food. We shall

in the following chapter discuss more fully the nature of the evidence that helps us to conjecture the existence of different sensation qualities in an animal's mind ; but it is clear that where an animal so simple in its structure as the *Amœba* makes no difference in its reactions to various stimuli, there can be no reason for supposing that if it is conscious, it is aware of them as different. The reaction to edible substances is, however, unlike that to other stimulations. The peculiarity of edible substances which occasions this difference must be a chemical one. In our own case, the classes of sensation which result from the chemical peculiarities of food substances are smell and taste ; evidently to a water-dwelling animal smell and taste would be practically indistinguishable. We may say, then, that supposing consciousness to exist in so primitive an animal as the *Amœba*, we have evidence for the appearance in it of a specific sensation quality representing the chemical or food sense, and standing for the whole class of sensations resulting from our own organs of smell and taste. The significance of the positive reaction is harder to determine. It seems to be given in response not to a special kind of stimulus, but to a mechanical or food stimulus of slight intensity. In our own experience, we do not have stimuli of different intensity producing sensations of different quality, except in the cases of temperature and visual sensations. We do, however, find that varying the strength of the stimulus will produce different *affective* qualities ; it is a familiar fact that moderate intensities of stimulation in the human organism are accompanied by pleasantness, and stronger intensities by unpleasantness. The motor effects of pleasantness and unpleasantness in ourselves are opposite to each other in character. Pleasantness produces a tonic and expansive effect on the body, unpleasantness a depressive and con-

tractive effect. In the *Amœba*, the positive and negative reactions seem to be opposed. The essential feature of the negative reaction is the checking of movement at the point stimulated; that of the positive reaction is the reaching out of the point stimulated in the direction of the stimulus. This much evidence there is for saying that besides a possible food sensation, the *Amœba* may have some dim awareness of affective qualities corresponding to pleasantness and unpleasantness in ourselves. It should, however, be borne in mind that wide differences must go along with the correspondence. In us, pleasantness brings a thrill, a "bodily resonance," due to its tonic effect upon the circulation, breathing, and muscles; unpleasantness has also its accompaniment of vague organic sensation, without which we can hardly conceive what it would be like. In an *Amœba*, it is clear that this aspect, as found in human consciousness, must be wholly lacking. Again, in the human mind pleasantness and unpleasantness are connected with various sensation qualities or complexes; we are pleased or displeased usually "at" something definite. The vagueness of the affective qualities in an *Amœba*'s consciousness can only be remotely suggested by our own vague, diffused sense of bodily well-being or ill-being; and this is undoubtedly given its coloring in our case by the structure and functioning of our internal organs.

As for the peculiar behavior of an *Amœba* suspended in the water and deprived of solid support, the stimulus for this must lie within the cell body itself. If any consciousness accompanies it, then the nearest human analogy to such consciousness is to be found in organic sensations, and these, as has just been said, must necessarily be in the human mind wholly different in quality from anything to be found in an animal whose structure is as simple as the *Amœba*'s.

A consequence of this lack of qualitative variety in the sense experiences of an Amœba is a lack of what we may call complexity of structure in that experience. The number of stimulus differences which are in the human mind represented by differences in the quality of sensations is so great that at any given moment our consciousness of the external world is analyzable into a large number of qualitatively different sensations. At the present instant the reader's consciousness "contains," apart from the revived effects of previous stimulation, many distinguishable sensation elements, visual, auditory, tactile, organic, and so on. The Amœba's consciousness, if it possesses one, must have a structure inconceivably simpler than that of any moment of our own experience.

A second point in which the mind of an Amœba must, if it exists, differ from that of a human being, consists in its *entire lack of mental imagery of any sort*. Not only has the Amœba but three or four qualitatively different elements in its experience, but none of these qualities can be remembered or revived in the absence of external stimulation. How may we be sure of this? If our primitive animal could revive its experiences in the form of memory images, it would give some evidence of the influence of memory in its behavior. Indeed, as we shall learn, it is possible, in all probability, for an animal's conduct to be influenced by its past experience even though the animal be incapable of reviving that experience in the form of a memory image. Therefore, if we find no evidence that the Amœba learns, or modifies its behavior as the result of past stimulation, we may conclude *a fortiori* that it does not have memory images.

Now it would be stating the case too strongly to say that past stimulation does not affect the behavior of Amœba at all. In the first place, this animal shows, in common with

all other animals, the power of "getting used" to certain forms of stimulation, so that on long continuance they cease to provoke reaction. "Thus," Jennings says, "Amœbæ react negatively to tap water or to water from a foreign culture, but after transference to such water they behave normally" (378, p. 20). Such cessation of reaction occurs when the continued stimulus is not harmful. In a sense, it may be called an effect of experience; but there is clearly no reason for supposing that it involves the revival of experience in the form of an idea or image. We have parallel phenomena in our own mental life. A continued stimulus ceases to be "noticed," but the process involves rather the disappearance of consciousness than the appearance of a memory image. Jennings, however, is inclined to think that preceding stimulation may modify the Amœba's behavior in a way more nearly suggesting memory in a higher type of mind. He describes an interesting observation to illustrate this. A large Amœba, *c*, had swallowed a smaller one, *b*, but had left a small canal open, through which the swallowed one made efforts to escape, which were several times foiled by movements on the part of the large Amœba toward surrounding it again. Finally it succeeded in getting completely out, whereupon the large Amœba "reversed its course, overtook *b*, engulfed it completely again, and started away." The small Amœba contracted into a ball and remained quiet until through the movements of the large one there chanced to be but a thin layer of protoplasm covering it. This it rapidly pushed through, escaped completely, and was not pursued by the large Amœba (378, pp. 17-18), (Fig. 3).

Of this performance Jennings says: "It is difficult to conceive each phase of action of the pursuer to be completely determined by a simple present stimulus. For example



FIG. 3.—Pursuit, capture, and ingestion of one Amoeba by another; escape of the captured Amoeba and its recapture; final escape. *b*, the captured Amoeba was originally a fragment of another. *A. J. S. 1900*

. . . after Amœba *b* has escaped completely and is quite separate from Amœba *c*, the latter reverses its course and recaptures *b*. What determines the behavior of *c* at this point? If we can imagine all the external physical and chemical conditions to remain the same, with the two Amœbæ in the same relative positions, but suppose at the same time that Amœba *c* has never had the experience of possessing *b*, — would its action be the same? Would it reverse its movement, take in *b*, then return on its former course? One who sees the behavior as it occurs can hardly resist the conviction that the action at this point is partly determined by the change in *c* due to the former possession of *b*, so that the behavior is not purely reflex" (378, p. 24).

If it is true that an Amœba which had not just "had the experience of possessing *b*" would not have reversed its movement and gone after *b* when the latter escaped, still we cannot think it possible that *c*'s movements in so doing were guided by a memory image of *b*. It may be supposed that the recent stimulation of contact with *b* had left a part of *c*'s protoplasm in a condition of heightened excitability, so that the weak stimulus offered perhaps by slight water disturbances due to *b*'s movements after escaping produced a positive reaction, although under other circumstances no reaction would have been possible. (Compare the observation of Schaeffer, just quoted, on Amœba's ability to react to objects not in contact with it.) In any case, there is no evidence that Amœba's behavior is influenced by stimulation occurring earlier than the moments just preceding action; no proof of the revival of a process whose original effects have had time to die out; and it is upon such revival that the memory images which play so much part in our own conscious life depend.

Let us consider for a moment some of the results of the

absence of this kind of material in the possible mental processes of *Amœba*. In the first place, such a lack profoundly affects the character of the experiences which the animal might be supposed to receive through external stimulation. If we call the possible conscious effect of a mechanical stimulus upon the *Amœba* a touch sensation, the term suggests, naturally, such sensations as we ourselves experience them. In normal human beings touch sensations are accompanied by visual suggestions, more or less clear, of course, according to the visualizing powers of the individual, but always present in some degree. Fancy, for example, one of us entering a room in the dark and groping about among the furniture. How constantly visual associations are brought into play! Not once is a mere touch impression apprehended without being translated into visual terms; the forms and positions of the articles encountered are thought of immediately as they would appear if the room were lighted. The difficulty we have in thinking of a touch sensation with no visual associations illustrates the difference between our sense experience and that of an animal incapable of recalling images of past sensations.

It is equally obvious that in the absence of memory ideas, not only must the *Amœba* lack processes of imagination and reasoning, but there can be nothing like the continuous self-consciousness of a human being, the "sense" of personal identity, which depends upon the power to revive past experiences. It is even possible that the "stream of consciousness" for an *Amœba* may not be a continuous stream at all. Since its sensitiveness to changes in its environment is less developed than that of a human being, and there are no trains of ideas to fill up possible intervals between the occurrences of outside stimulation, the *Amœba*'s conscious experience may be rather a series of

"flashes" than a steady stream. And for the Amoeba, again, we must remember that even such a series would not exist as such; the perception of a series would involve the revival of its past members. Each moment of consciousness is as if there were no world beyond, before, and after it.

Another consequence of that simplicity of structure which results both from the rudimentary powers of sensory discrimination and from the absence of memory ideas in the Amoeba's mind is that there can be no distinction, within a given mental process, between that which is attended to and that which is not attended to, between the focus and the margin of consciousness. Given a consciousness which at a certain moment is composed of the qualitatively different elements *A*, *B*, *C*, and *D*, we can understand what is meant by saying that *A* is attended to, is in the foreground of attention, while *B*, *C*, and *D* remain in the background. But given, on the other hand, a creature whose conscious content at a certain time consists wholly of the qualitatively simple experience *A*, it is evident that attention and inattention are meaningless terms. Different moments of its consciousness may differ in intensity; but attention, involving, as it does, clearness rather than intensity, arises only when mental states have become complex and possess detail and variety within their structure.

CHAPTER IV

SENSORY DISCRIMINATION: METHODS OF INVESTIGATION

§ 10. *Preliminary Considerations*

ONE of the most important points in which the human mind differs from the mind of the lowest animal forms consists, we have seen, in the enormously greater number of different sensations which enter into human experience, as compared with the small number of sensory discriminations possible to the simpler animals. Much of the experimental work that has been done on animals has been directed toward discovering what discriminations they make among the stimuli acting upon them, and to the results of this work we shall give our attention in the next chapters. But first we ought to get a clearer idea of just what kind of evidence is needed to indicate the existence of a variety of sensations in an animal's mind.

At the outset, we must remind ourselves that, in the absence of any satisfactory proof that the lower animal forms have minds at all, and the equal absence of any proof that they have not, all our conclusions about the number and kind of their possible sensations must remain subject to the proviso that they possess consciousness. Further, a point that was mentioned in Chapter I must again be emphasized. No evidence of discrimination between two stimuli on an animal's part can do more than show us that for the animal they are different; just what the quality of the sensation resulting from each may be, whether it

is identical with any sensation quality entering into our own experience, we cannot say. The light rays which to us are red and blue may for an animal's consciousness also differ from each other, and yet if our experience could be exchanged for the animal's, we might find in the latter nothing like red and blue as we know them.

Thus much being premised, what sort of evidence can be obtained that an animal does discriminate between two stimuli? Again, as in considering the evidence for the existence of consciousness in general, there is an argument from structure and an argument from behavior.

§ 11. *Structure as Evidence of Discrimination*

The *argument from structure* consists primarily in the fact that an animal possesses sense organs recognizably like our own. If a creature has an organ suggesting strongly the construction of the human cochlea, or an organ with a lens and a membrane composed of rods and cones, it is highly probable that auditory stimuli in the one case and light in the other produce specific sensations. This argument from the morphology of sense organs is, however, limited in two ways. First, it is only a small part of the animal world whose sense organs resemble ours closely enough to make the analogy safe. And secondly, we do not after all know very much about the relation of our own sense-organ structure to function. We know, for example, that our own organ with a lens and retina gives us visual sensations, but we cannot say with certainty which structures in the retina furnish brightness sensations and which color sensations, nor do we know anything about the retinal structures that underlie different qualities of color sensations. We can say that sensations of hearing come

from the ear, but no one can tell us how to judge from the structure of the ear what range and fineness of pitch discriminations exist in its possessor's mind. No investigator has yet succeeded in relating the different qualities of smell and taste to differences in the end organs.

§ 12. *Behavior as Evidence of Discrimination*

The *argument from behavior* is as follows: If an animal reacts in a different way to two qualitatively unlike stimuli, then, providing that it is conscious at all, it may be supposed to receive qualitatively unlike sensations from them. If it always reacts in the same way to both, then both may be supposed to be accompanied by the same sensation quality. Obviously these statements need further discussion. For one thing, it may be urged that in our own case the same external reaction is often made to stimuli that are nevertheless consciously discriminated. A man may eat with relish and without observable difference in behavior, for example, foods that yet give him perfectly distinguishable smell and taste sensations. Precisely this objection holds against a method of experimentation, formerly a good deal used, which may be called the Preference Method of testing discrimination. Vitus Graber, for instance, attempted to find whether animals belonging to a variety of species could discriminate colors, by offering them the choice of two compartments illuminated each with a different color. Clearly, if the animals chose one compartment as often as the other, it would be rash to conclude that the two lights produced for them indistinguishable sensation qualities. There might simply be the absence of any preference, along with perfect discrimination. The fact is that in all experiments upon animals, whether

to determine their power of distinguishing stimuli or their power of learning by experience, the first requisite is to give the animal what we commonly call a *motive*. That is, the conditions of the experiment must be so arranged that some already present tendency to act, whether inborn in the animal or acquired by previous experience, shall be appealed to.

This is increasingly the case, the higher the animal worked with stands in the scale. The higher animals have what might be called a large reserve fund of discriminations. That is, they are capable of making many more selective reactions to stimuli than they need at a given moment actually to use. Hence in their case the experimenter must make a careful adjustment of conditions to bring out exactly the discrimination wanted. He must either make the performance of the reaction pleasant or its non-performance unpleasant to the animal. A monkey, for example, confronted by a set of glass tumblers covered each with a differently colored paper, may behave toward them all in precisely the same way; yet if food be put regularly in the blue tumbler, whose position in the row is varied, it becomes worth the monkey's while to make use of his discriminative powers, and he may show by his different behavior toward the blue tumbler that it produces on him a different impression from the others.

With simpler animals the problem is less difficult. If an animal is capable only of a half dozen different ways of responding to stimulation, we may with comparative safety assume that it has less opportunity to hold them in reserve; and if such an animal invariably reacts in the same way to two different forms of stimulus, or if the variations in its response are not correlated with differences in the stimulation, it becomes probable that the two

stimuli produce in its assumed consciousness identical sensation qualities. Thus it is not the number of stimuli to which an animal reacts that can be taken as evidence of the qualitative variety of its sensations, but the number of stimuli to which it gives different reactions. When Jennings, for instance, says that *Amœba* "reacts to all classes of stimuli to which higher animals react" (378, p. 19), we cannot conclude that it possesses all classes of sensations that higher animals possess, for its reactions to these different stimuli are but little varied according to the kind of stimulus.¹

An ingenious way of getting evidence from behavior is the salivary reflex method devised by the Russian physiologist Pawlow (830). The salivary ducts of the dog, which lie near the surface, are operated on so that the saliva can be discharged into a graduated tube. As is well known, the sight or smell of food increases the flow of saliva. Now when any other stimulus, such as a sound, regularly accompanies the sight or smell of food, this stimulus, originally without effect on the salivary flow, comes to increase the flow even in the absence of food. If, now, the stimulus that has thus acquired the power to affect the salivary flow is given in irregular alternation with another stimulus differing slightly from it, and the other stimulus is found not to affect the flow of saliva, then the inference can be drawn that sensory discrimination between these two stimuli is possible for the animal. It is maintained by some investigators that when sensory discrimination can be studied through such simple types of behavior

¹ One of many reasons for the unsatisfactoriness of an article by A. Ölzelt-Newin, entitled "*Beobachtungen über das Leben der Protozoen*" (529), lies in the author's uncritical acceptance of the hypothesis that reaction to a special kind of stimulus means a special kind of sensation.

as the salivary and other reflexes, there is less chance of misinterpretation than when more complicated choice processes are involved.

In all experiments where behavior alone is the basis of inference regarding sensory discrimination, we need to take the utmost care that the animal is really responding to the stimuli, and not to some other accidental cue. Thus a dog in the Harvard laboratory was apparently discriminating accurately between two lighted areas of different size, but events proved that he was actually responding to slight pulls given by the experimenter on the leash that held him. He failed wholly when he was taken off the leash. Nowadays the careful experimenter always remains out of sight and hearing of the animal tested, and is not in contact with it in any way.

§ 13. *Evidence from Structure and Behavior Combined*

As a matter of fact, the argument from structure needs confirmatory evidence from behavior. For clearly the mere presence of a sense organ bearing sufficient likeness to our own to admit of conjecturing its function would be of no value as proof unless it were shown that the sense organ actually functioned. In order to do this, it would be necessary to show that the animal reacted to the stimulus conjectured as appropriate to the sense organ, and that removal of the organ profoundly modified the reaction. Thus we shall find that many experiments to test sensory discrimination have been made by the *method of extirpating a sense organ* and studying the effect on behavior. The method has many disadvantages, the chief of which lies in the fact that it is hard to say which disturbances in behavior are due actually to the loss of the organ and

which to the more widespread effects of the operation. Yet this much may be said for the combination of proof from structure and behavior involved in the Method of Extirpation, if we may so call it: where an animal reacts to a certain stimulus, for instance light, when a sense organ is intact, and fails to react to light, though otherwise normal, when the organ is removed, there arises a possibility that light may produce in the animal's consciousness a specific sensation quality, *even although the animal ordinarily reacts to light in a manner indistinguishable from that of its responses to other stimuli*. Though light and mechanical stimulation, for example, both ordinarily produce a negative reaction, yet if light brings about its effect only through the medium of a specialized structure with which mechanical stimuli are not concerned, then along with the probable unpleasantness accompanying the negative reaction there may go a quality peculiar to the functioning of that special structure.

Another mode of combining evidence from structure with evidence from behavior is by the *use of localized stimuli*. If an animal gives a response, which in itself may have nothing to mark it off from responses to other stimuli, when a special kind of stimulation is applied to certain regions of the body, and only then, while the other stimuli produce better reactions when applied elsewhere, then the suggestion is given that different sense organs are involved, and the same possibility arises of different sensation qualities.

Two other forms of evidence whereby from behavior a differentiation of sensory structures can be argued, and from differentiation of sensory structures possible differences of sensation quality, may be mentioned. The first of these consists in showing that reactions to different

stimuli may be *independently fatigued*. The natural inference is that a specific nervous apparatus belongs to each stimulus. The second lies in demonstrating that the reactions to different stimuli occur with different degrees of rapidity. If there is a marked *difference in the reaction times* of an animal to different forms of stimulation, each, again, may be supposed to affect its own nervous pathway. A modification of this method consists in noting the influence of a stimulus upon the time of reaction to another nearly simultaneous stimulus. If such an influence can be shown, it is evident that the force producing it has some effect on the nervous system. By combining this method with that of extirpating a sensory structure, indications may be obtained that the nervous effect of the auxiliary stimulus is dependent on a definite receptive apparatus, and hence is probably accompanied by a special sensation. This method was used by Yerkes to demonstrate hearing in frogs (813).

One further consideration offers itself to the student of animal responses to stimulation. It has been the special endeavor of Jennings to point out the fact that these responses, instead of being wholly accounted for by the characteristics of the stimulus, are determined in part by the internal, physiological condition of the animal (378). We shall therefore note often in the course of the following pages cases where difference of reaction is due to internal rather than to external causes.

§ 14. *Evidence for Discrimination of Certain "Lower" Sensation Classes*

Bearing all these points in mind, let us proceed to survey the evidence for variety in the sensations of animals. In

the lowest forms, such evidence must be derived entirely from behavior. That from the presence of a sense organ is almost wholly lacking. And although various stimuli, as we have seen, produce reactions in *Amoeba*, yet there is only one case where these reactions are strikingly different according to the quality of the stimulus applied. This instance consists in the distinction between food-taking reactions, given to edible substances, and the responses to mechanical stimulation. The sense of touch, undoubtedly, must play a part in the mental life of the lowest animals that have consciousness at all. But the earliest distinction between a touch quality and a quality that is other than touch seems to occur when food sensation and contact sensation are differentiated. It is possible that warmth and cold also appear as distinct sensation qualities in the experience of low forms of animals, but we have little real evidence of the fact. No organs of temperature sensation are definitely known even in human beings. And the responses of low animals to thermal stimulation are not specialized. They consist usually of negative reactions, given when the animal is subjected to a temperature either above or below, but especially above, the "optimum"; and these reactions are not different from the ordinary negative type, suggesting unpleasantness rather than a specific sensation quality. In some cases the sensibility to thermal stimulation has been found to be differently distributed from that to other classes of stimuli. But in any case, sensations of warmth and cold are probably in no member of the animal kingdom differentiated into any greater number of qualitatively distinct sensations.

The sense of touch, also, shows but little internal differentiation. Its importance, so far as we can judge, is

rather on the spatial than on the qualitative side. The sense quality of pain we naturally think of as the accompaniment of the negative reaction in its more violent forms, given to a stimulus that is injuring the organism. Organic and kinæsthetic sensations are hard to trace in the lower animals; for animals whose structure differs widely from our own, the qualities of these two classes must remain beyond the power of our imagination. That differences in physiological condition such as are produced by hunger, satiety, or fatigue involve differences of accompanying organic sensation in the consciousness of the animal manifesting them is possible. Kinæsthetic sensations, as we shall see, are apparently concerned in the processes whereby many animals have learned to traverse a labyrinth path.

The three classes of sensation whose existence in the animal mind can be most satisfactorily traced are the chemical sense, under which smell and taste belong, the sense of hearing, and the sense of sight. To the study of these the following chapters will be devoted. Since the manifestations of the chemical sense in the lowest forms of animals consist chiefly in a differentiation of response to food and to mechanical stimulation, the contact sense or sense of touch will, in discussing these forms, be considered along with the chemical sense.

CHAPTER V

SENSORY DISCRIMINATION: THE CHEMICAL SENSE

§ 15. *The Chemical Sense in Protozoa*

WE have already seen that the most primitive type of protozoön, *Amæba proteus*, discriminates between edible and inedible substances. While it will sometimes 'swallow' inedible particles such as grains of carmine, it takes immediate measures to get rid of them, measures too prompt to be the result of an actual attempt at digestion, and hence properly to be regarded as the effect of a chemical or food sense. Many other members of the lowest division of the animal kingdom, the Protozoa, have a structure and behavior decidedly more complicated than those of *Amœba*. There is a large group of single-celled animals called Ciliata, from the fact that their bodies are covered with little hair-like protoplasmic filaments or cilia which serve as organs of locomotion by acting like tiny oars. A common representative of the group is *Paramecium*. The structure of this animal is distinctly more specialized than that of *Amœba*. Not only are the cilia modified locomotory structures, but there is a definite region for food-taking. A groove extends obliquely down one side of the body, terminating at its lower end in a mouth. The cilia along this oral groove beat with especial vigor and create currents which sweep food particles to the mouth. *Paramecium* swims rapidly through the water with a spiral motion of its body, due to the facts that the aboral cilia beat more

strongly than the rest, and that the animal compensates for the turning thus occasioned by turning on its long axis. Its reactions to stimulation Jennings has shown to be only two in number. First, there is a very definite avoiding or negative reaction. This is given in response to decided mechanical stimulation at the anterior end, as when the animal swims rapidly against an obstacle, and also in response to chemical stimulation, to strong ultra-violet rays (299), and to temperatures above or below a certain middle region called in this case, as in analogous cases with other animals, the *optimum*. For *Paramecium* it lies between 24° and 28° C. The negative reaction consists, according to Jennings, of the following process: the animal darts backward, reversing the beat of its cilia, turns toward the aboral side (that opposite to the oral groove) by increasing the beat of the oral cilia and lessening the compensating rotation, and continues on a forward course that is now at an angle with its former line of motion. If this new course carries it clear of the stimulus, it continues on its way; if not, repeated contact with the stimulus causes a second reaction, the *Paramecium* always turning in the same direction, so that ultimately it avoids the source of stimulation (361, 378) (Fig. 4). Differing strengths of stimulus produce the reaction with different degrees of violence. When a very strong stimulus is encountered, the animals "respond first by swimming a long way backward, thus removing themselves as far as possible from the source of stimulation. Then they turn directly toward the aboral side, — the rotation on the long axis completely ceasing. In this way the animal may turn directly away from the drop [the stimulus] and retrace its course" (378, p. 50). On the other hand, when the stimulus is very weak the reaction may be reduced to the

following form: the Paramecium "merely stops, or progresses more slowly, and begins to swing its anterior end about in a circle." As long as it does not thus get out of range of the stimulus, the movement is continued. "When the anterior end is finally pointed in a direction from which no more of the stimulating agent comes, the Paramecium swims forward" (378, p. 51). Evidently, however, these are but differing degrees of a reaction whose essential features are the same.

While Paramecium definitely avoids by means of this

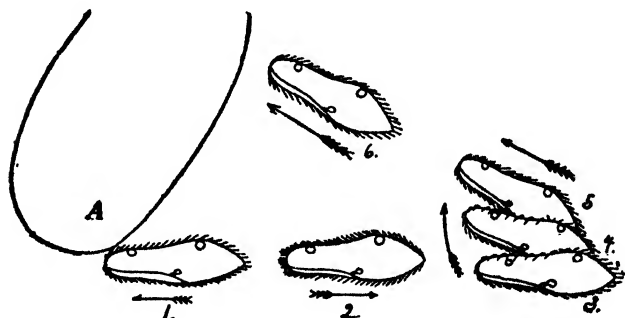


FIG. 4. — Negative reaction of Paramecium. A is the source of stimulation. 1-6 are the successive positions of the animal. After Jennings (378).

negative reaction certain chemicals introduced into the water, it shows a tendency to collect in the neighborhood of others. Such is the case with weak acids, with a bubble of oxygen if air has been long excluded from the slide, and with carbon dioxide, which in water of course produces acid (378). Jennings pointed out that the inclination of Paramecium to gather in groups is very likely due to the attraction for them of the carbon dioxide which they excrete. But he has also shown that this "attraction" to certain chemicals does not mean the presence of a special

positive reaction. The fact is that when the animals collect in a drop of weak acid, for example, they are not drawn toward the acid. They simply happen, in their ordinary movements, to swim into it, and on entering it show no disturbance whatever. But when they come to the edge of the drop on their way out, they give the negative reaction to the surrounding water. In this way they are, as it were, trapped within the drop.



FIG. 5. —
Positive
thigmotaxis
in *Paramecium*. After
Jennings
(378).

The nearest analogue to a positive reaction in *Paramecium* consists in the fact that sometimes, when they come into contact with a solid, instead of darting backward, the animals merely cease moving, and extending stiffly the cilia which touch the object, remain at rest (Fig. 5). The utility of this behavior is that around decaying vegetable matter, the kind of solid oftenest found in the animal's ordinary environment, there is apt to be a supply of food in the way of bacteria; it is a good anchorage. What characteristics of the stimulus determine that this "contact reaction," rather than the negative reaction, shall be given? Does weak mechanical stimulation occasion it, as happens with *Amoeba's* positive reaction? Evidence in favor of this is offered by the fact that the contact reaction is more likely to occur if the animal comes against the solid when swimming rather slowly. Jennings reports also that individuals vary. "Often all the individuals in a culture are thus inclined to come to rest, while in another culture all remain free-swimming, and give the avoiding reaction whenever they come in contact with a solid" (378, p. 60). This would suggest that some individuals are in a state of greater excitability than others, so that a

given stimulus acts more strongly upon them. On the other hand, there is a possibility that qualitative as well as intensive differences in the stimulus are responsible for the contrasting reactions. "In general," says Jennings, *Paramecium* "shows a tendency to come to rest against loose or fibrous material; in other words, it reacts thus to material with which it can come in contact at two or more parts of the body at once. To smooth, hard materials, such as glass, it is much less likely to react in this manner" (378, p. 61). Perhaps, then, the spatial distribution of the stimulus over several points of the body surface increases the probability of a contact rather than an avoiding reaction.

What, now, of the food-taking reaction in *Paramecium*: does it show evidence of the existence of chemical discrimination? When the animal finds itself in surroundings where certain presumably injurious chemicals, especially alkalis, are present, it gives its typical negative reaction. If this should be called evidence of a special chemical sense, we should be forgetting our general principle that only unlike reactions constitute behavior indicating sensory discrimination. Since *Paramecium* reacts in the same way to strong mechanical stimulation and to certain chemical stimulations, there is no reason for assuming a discrimination between chemical and mechanical stimuli. If it can be shown that the reaction is a localized one, that the cilia which surround the mouth reverse the direction of their beat when certain kinds of particles strike upon them, with the result that these particles are thrown out, then the question as to the existence of a chemical discrimination would depend on whether the rejected particles are chemically unlike those which are accepted, or different only in size or mechanical consist-

ency. Jennings (378) reports no such rejection of unsuitable particles in the case of *Paramecium*, but Metalnikow (485, 486) says that when *Paramecia* have been kept for some time in water containing carmine grains they cease to swallow them; the evidence being that fewer and fewer grains are found in the animals. Schaeffer (656) thinks this result is due to the mechanical change in carmine grains that have been long in the water, which become stuck together in the mucus excreted by the *Paramecia*. Metalnikow (487) however finds that when fresh carmine is used the *Paramecia* avoid it apparently as a result of their previous surfeit, and that when particles of aluminum are used instead of carmine they acquire a discrimination against these even more quickly. He therefore feels convinced that the discrimination is a chemical one.

Stentor is a ciliate protozoön which spends a part of its existence anchored by a long extension of its body, like the stem of a flower: at times it pulls this up and swims off. Food is taken in by the whirl of cilia around the mouth, and may be rejected by a reversal of the direction of this whirl. Schaeffer (656) says that *Stentor* discriminates not only between organisms and inedible particles, but between different kinds of organisms; he thinks, however, that the basis of discrimination is not chemical, because food soaked in a variety of chemicals is readily taken, while jelly made of food organisms is rejected. He believes the discrimination rests probably on several mechanical factors in combination, for example, size, weight, form, and surface texture, no one of which is alone sufficient to determine the choice. On the other hand Lund (446), observing another ciliate named *Bursaria*, finds that this organism will reject yolk of egg particles if they have been treated with certain dyes, and concludes that the basis

of discrimination is chemical. *Lacrymaria*, another ciliate, tests with its 'head' "every object within reach and rejects all those which cannot serve as food. It does not swallow inorganic substances, carmine, or ink particles and the like. This protozoön unquestionably exercises selection in feeding" (469, p. 243), but the basis of the selection is not determined. *Didinium* is a ciliate which has a peculiarly modified seizing organ, but the only selection of food which it makes rests on the fact that this organ will adhere to the surface of some organisms and not to that of others (466). Two other protozoa, *Actinobolus radians* and *Spathidium spathula*, have each so far refined the process of selection of food that they swallow only one kind of organism. *Actinobolus*, an anchored form, awaits its destined prey, and *Spathidium* selects it in freely swimming about; but as to whether the prey is recognized by chemical or by mechanical features we have no information (499).

§ 16. *The Chemical Sense in Cœlenterates*

The lowest of the Metazoa, or many-celled animals, are the cœlenterates. Although externally the forms of different families of cœlenterates differ widely, yet the general plan of structure is the same in all: the body of the typical cœlenterate is a hollow sac, whose walls consist of two layers of cells, food being taken into a mouth at one end of the sac, and the arrangement of cells being on the plan of circular symmetry. In the phylum of the cœlenterates are included sea-anemones, jellyfish, the little green or yellow *Hydra*, sponges, corals, and ctenophores.

Hydra (Fig. 6), one of the simplest cœlenterates, shows a food reaction distinct from the contact reaction. Mechanical stimulation is followed by withdrawal of the ten-

tacles and by contraction of the stem. This behavior may be called a negative or avoiding reaction, and no positive reaction to a mechanical stimulus has been observed. The food-taking reaction, on the other hand, consists in the seizing of the food by the tentacles. It

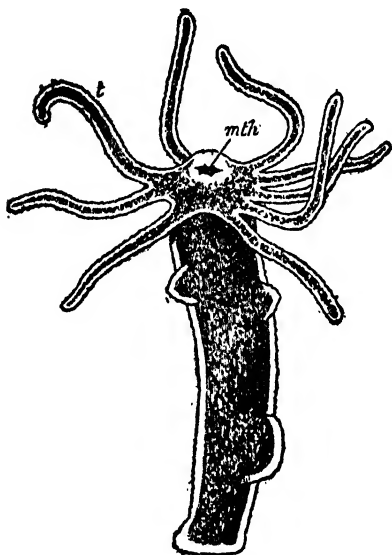


FIG. 6.—Hydra. *mth*, mouth; *t*, tentacle.
After Parker.

seems to be given in response to a combination of chemical with mechanical stimulation, such as is offered by contact with a solid edible object (751 a). Shall we say that Hydra possesses, then, a food sensation and a contact sensation that are distinguishable in its consciousness, provided such consciousness exists? It may be that the contrast between the two is more nearly analogous to that between pleasantness and

unpleasantness in our own experience, for the food-taking reaction in Hydra is the only form of the positive reaction, and the response to mere contact is distinctly negative in character. The influence of *physiological condition* in Hydra's reactions is shown by the fact that although ordinarily the food response is brought about only by contact with food, if the animal is very hungry any chemical stimulation, even quinine, will produce it (751 a). This blunting of discrimination has, of course,

the adaptive aspect that the starved animal can afford to lose no chances, and suggests the analogy from our own experience of the loss of intellectual discrimination in moments of intense emotion. For the emotion too represents a situation where the organism cannot afford to lose chances by hesitating in reaction long enough for nice discrimination.

In *Tubularia crocea*, a coelenterate belonging to the family of hydroids which form colonies of many individuals on a common stem, food and contact stimuli do not produce different reactions, but have different degrees of efficiency in bringing about response. When a grain of sand was placed in contact with the tentacles on one side and a bit of meat in a corresponding position on the other side, the reaction was almost invariably in the direction of the meat. Filtered meat juice allowed to flow upon the distal tentacles produced a reaction 82 per cent. of the time, while carmine water was effective only 15 per cent. of the time. Further, if the distal tentacles were touched several times with a needle, they remained closed; but if the second stimulus used was a piece of meat, the tentacles opened out and waved about (564). Whether in such a case as this the possible conscious accompaniments of the responses are to be regarded as qualitatively different sensations, or only as different degrees of intensity of the same sensation, it is difficult to say. Another hydroid, *Corymorpha palma*, gives no response whatever to meat juice; only irritating chemicals produce reactions, whose character appears to be tactile (714).

In the sea-anemones or actinians we find behavior in response to food stimulation as distinguished from contact stimulation varying in different representatives of the group. Generally speaking, the food reaction seems to

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be more marked than the contact reaction. W. H. Pollock a number of years ago reported his observation that certain unnamed sea-anemones opened out if food were suspended near them in the water, and referred the phenomenon to "a sense of smell" (609). *Adamsia rondeleti* winds its tentacles around bits of sardine meat and passes them from tentacle to tentacle toward the mouth. When balls of filter paper softened with sea water are substituted, the feeding reaction is wholly lacking. Either the tentacles fail to react at all, or the ball is "felt of" slowly with no attempt to seize it, or it is momentarily seized and then dropped. If the paper ball be soaked in fish juice, on the other hand, it is seized as eagerly as the fish meat. A negative reaction, consisting in the withdrawal of the tentacles affected, may be produced by applying a bit of paper soaked in quinine solution or by the discharge of quinine solution from a pipette near the tentacles (427, 518). A peculiar form of negative reaction has been observed in *Adamsia*, and more strikingly in *Cerianthus*, when a paper ball soaked in fish juice has been passed from tentacle to tentacle till it has nearly reached the mouth. The process is suddenly reversed, and the ball is passed back from one tentacle to another till it reaches the outside edge and is dropped off. Nagel, the observer, thinks the stimulus for this change of reaction is the gradual wearing off of the "sapid parts" of the ball during its passage toward the mouth — it might be the squeezing out of the meat juice — and calls special attention to the fact that the reaction whereby the paper is got rid of is wholly different from the ordinary reaction of a tentacle to mechanical stimulation, which, as we have seen, does not involve seizing the object at all. A tentacle touched by a bit of moistened filter paper ordinarily responds, if at all, by a mere

contraction without the winding seizure of the object. Touched by the same object "handed on" to it by a tentacle nearer the mouth than itself, it seizes the paper and passes it on to the tentacle beyond it. The cause of this difference in behavior seems to lie in the processes that have been taking place just previously. Nagel does not hesitate to say that a psychic process must be involved, but its details are not easy to construct (521).



FIG. 7. — Metridium. After Parker.

Another sea-anemone, *Aiptasia*, has but one ring of tentacles, and like *Tubularia crocea*, instead of showing different responses to contact stimulation alone and to contact plus food stimulation, it merely reacts with greater emphasis to the latter. In both cases the tentacles wind around the object, contract, and direct themselves toward the mouth (521). Again the question arises whether the possible accompanying sensations differ in quality or only in intensity. One species of *Aiptasia*, *A. annulata*, however, does react differently to filter paper soaked in crab juice and to plain filter paper (374), showing that even within a genus the capacity for stimulus discrimination may differ. In like manner one sea-anemone, *Actinia*, will take filter paper soaked in acetic acid, while another, *Tealia*, rejects it (228).

Metridium, a common sea-anemone of our coasts, has its tentacles covered with cilia which have a continual waving motion toward the tip of the tentacle (Fig. 7). If particles of an inedible substance are dropped on a tentacle, no definite reaction occurs, but the particles are carried by the ordinary motion of the cilia out to the ten-

tacle tip, where they drop off. When a bit of crab meat, or some meat juice, is dropped on a tentacle, the latter contracts and curls over with the tip directed toward the mouth. The ciliary movement continuing in its usual direction now of course carries the food toward the mouth. Applying food to the lips on either side of the mouth causes a different response. The cilia on these lips ordinarily wave outwards; when food is brought in contact with them their motion is reversed, and the food is thus passed into the mouth. In *Metridium*, then, there is no specific rejecting reaction for inedible substances (533).

Various instances of the *effect of physiological condition* upon response to food stimulation in sea-anemones have been noted. *Adamsia* loses the power to discriminate between edible and inedible substances when very hungry (521). *Sagartia darisi* will also swallow inedible substances if hungry enough (715). *Stoiachactis helianthus* will give either a positive or a negative reaction to food according to its condition of hunger or satiety (374). The reaction of *Metridium* to food may vary decidedly with the degree of hunger (3), although it will continue taking food as long as the process is mechanically possible (378). Fatigue has also been shown to affect the food responses of *Metridium* and other sea-anemones; specimens that have been fed meat and filter paper alternately will after a time refuse to take filter paper (374, 521, 533). This behavior was thought by Nagel to indicate that the animal had discovered the deception practised upon it; but according to Gee (256) the real cause is increased secretion of mucus, which lowers the responsiveness of the animal. This effect would naturally be felt first in response to weak stimuli.

As regards the localization of the sensitive elements,

authorities disagree, and probably species differ. Nagel finds the tentacles most sensitive (521); Loeb observed that the stump of the animal has discriminative reactions (427), while Fleure and Walton state that in the species tested by them the mouth-region is most responsive to chemical stimulation (228).

A certain amount of discrimination between mechanical stimuli is ascribed to these animals by Romanes. "I have observed," he says, "that if a sea-anemone is placed in an aquarium tank and allowed to fasten upon one side of the tank near the surface of the water, and if a jet of sea water is made to play continuously and forcibly upon the anemone from above, the result of course is that the animal becomes surrounded with a turmoil of water and air bubbles. Yet after a short time it becomes so accustomed to this turmoil that it will expand its tentacles in search of food, just as it does when placed in calm water. If now one of the expanded tentacles is gently touched with a solid body, all the others close around that body in just the same way as they would were they expanded in calm water" (642, p. 48), although the solid stimulus is decidedly less intense than that offered by the bubbles. Similarly, Fleure and Walton find that certain species show little reaction to accidental contact with a pebble that is moved, but react quickly to a finger (228).

The body of a typical medusa or jellyfish consists of a bell-shaped "umbrella" from the edge of which tentacles depend. Hanging from the middle like the clapper of the bell or the handle of the umbrella is the manubrium, at the end of which is the mouth. In the medusa *Carmarina hastata* no differentiation in reaction to contact and food stimulation appears, merely a readier response of the tentacles to the latter; but we do find whatever evidence for

the existence of a specific sensation quality is furnished by localized sensitiveness, for the skin of the under side of the umbrella, and of the manubrium, is very sensitive to mechanical stimulation, and wholly insensitive to chemical stimulation, while the tentacles, as has just been stated, react, by shortening and twisting themselves about the

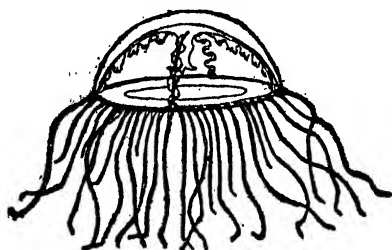


FIG. 8.— *Gonionemus*. After Hargitt.

object, more readily to chemical than to mechanical stimulation. A mechanical stimulus applied to any part of the under edge of the umbrella produces after from one to three seconds a movement

of the manubrium tip toward the point stimulated (519, 521).

The little medusa *Gonionemus murbachii* (Fig. 8) shows, on the other hand, two well-defined different responses to special stimulation: motor reactions and food-taking reactions. The motor or swimming reactions are given in response to mechanical stimulation and to the presence of food near the animal in the water; but the food-taking reaction occurs only in response to food (solution of fish meat); very rarely a weak inorganic chemical stimulus will produce the beginning of the response. An important exception to the usual inefficacy of mechanical stimuli in bringing about the feeding reaction occurs when a *moving* mechanical stimulus is used; this very quickly produces the early stages of the food-taking response. Special reactions to stimuli in motion are widespread throughout the animal kingdom; their significance will be discussed in the chapter on Space Perception. The food-taking re-

sponse in *Gonionemus* shows a marked coördination of movements; if the food touches one or more tentacles, these contract and twist about it; they then bend toward the manubrium, and the margin of the bell also bends in; the manubrium swings over toward the bell and envelops the food with its lips (802).

Another cœlenterate whose reactions to chemical stimulations have been observed is the ctenophore *Beroë ovata*. Its body is an elongated oval, with longitudinal ciliated ridges, having the mouth slit at the end which is normally uppermost when the animal is at the surface of the water, and at the opposite end an otolith or statolith organ lying between two flattened "polar plates." The significance of this organ will be considered later. The aboral region is far more sensitive than any other to mechanical stimulation; the slightest touch on one of the polar plates causes the animal to shorten itself and fold in the plates. The aboral end, being the hind end of the creature, is not usually brought into contact with objects. Nagel, who studied the animal, suggests that this region, being sensitive to changes in pressure, may enable the animal to right itself when it rises to the surface with the aboral end up, as the change from water to air pressure could not fail to stimulate the polar plates. Nagel apparently made no experiments on the behavior of *Beroë* with reference to food stimuli; for chemical stimulation he used picric acid, dilute hydrochloric acid, quinin, strychnin, saccharin, coumarin, vanillin, and naphthalin. To all these unwonted stimuli the animal responded by some form of negative reaction, indicating possible unpleasant feeling. The edges of the mouth, where the nerves end in bulb-like structures, reacted to quinin, vanillin, and coumarin by stretching the mouth into a circular form instead of its

usual slit-like shape, suggesting an effort to get rid of the stimulus. Precisely similar reactions were produced by stimulation with lukewarm water. Nagel concludes that the organs for chemical and thermal stimulation are identical; whether the sensation qualities are different is, he thinks, an open question. There is at least no evidence that they are different (519, 521).

§ 17. *The Chemical Sense in Flatworms*

Next to the coelenterates zoölogists place the phylum of the Platyhelminthes or flatworms, which possess a bilaterally instead of a radially symmetrical structure. Many representatives of the group are parasitic, and so far as the writer is aware, no extended study of the reactions of these forms to stimulation has been made. Most of our knowledge in regard to the sensory life of the flatworms is confined to the class Turbellaria, including the common freshwater and marine planarians. These are small slow-moving creatures which crawl about on solid objects under water or on films covering the surface. The mouth is situated on the ventral side of the body, sometimes quite far removed from the head end (Fig. 9). One chief interest of planarians to physiologists has lain in their remarkable power to regenerate parts lost by mutilation.

Planaria maculata, a common freshwater planarian, responds to stimulation by two forms of negative reaction, a positive reaction, and a feeding reaction. The negative and positive responses are given either to mechanical or to chemical stimuli, the former being produced by strong, the latter by weak stimulation. Hence they do not suggest correlation with qualitatively different sensation contents, but rather with unpleasantness and pleasantness.

The two forms of negative reaction correspond to differences in the location of the stimulus. If the head end of the body is stimulated strongly on one side, the head is turned away from that side. If the posterior part of the body is strongly stimulated, the animal makes powerful forward crawling movements. The significance of local differences in stimulation for response and for possible consciousness, again, will more properly be discussed in a later chapter. As has just been said, both weak chemical and weak mechanical stimulation cause *Planaria maculata* to give a positive reaction by turning its head in the direction of the stimulus, which need not be in actual contact with the body (561). A planarian will follow an object such as the point of a pin moved in front of it, and one planarian will follow the trail of another that happens to come within the proper distance. Similarly, the neighborhood of food will cause the animal to turn toward it. Bardeen has suggested that the so-called "auricular appendages," two small movable prominences on the animal's back near the head end, which are specially sensitive to touch, may be "delicate organs capable of stimulation by slight currents in the water set up by the minute organisms that prey" upon the animal's food; so that the positive reaction when given to food may be really a response to mechanical stimulation (20). As Pearl, however, found that chemicals, diffused in the water, would produce positive responses (561), it is probable that *Planaria*



FIG. 9. — Planarian, dorsal view. After Woodworth.

maculata is directly sensitive to chemical stimulation, though it responds thereto in the same way as to mechanical stimulation. A land planarian, *Geodesimus bilineatus*, is reported by Lehnert to perceive food at distances from four to five times the length of its body, and he does not describe the positive reaction as given in response to any other than food stimulation (417).

The food-taking reaction in *Planaria maculata* is made under the influence of combined mechanical and chemical stimuli, in contact with the pharynx or the ventral side of the animal. When an object which has occasioned the positive reaction is reached, the head folds over it and grips it, contracting so as to squeeze it. The substance being thus brought into contact with the pharynx, swallowing movements are produced if the proper stimulus is given. In *Microstoma caudatum* the organ of the chemical sense has been held to be sensory epithelium in the floor of the pharynx (398). Bardeen was inclined to think that contact with a soft substance constituted the proper stimulus, as he found that hard particles placed on the pharynx were not swallowed (20). Pearl, however, believes that mechanical and chemical stimulation must combine. The former alone does not suffice, for swallowing movements are not evoked when one planarian crawls over another; the latter alone is insufficient, for placing the animal in a sugar solution has no effect. If chemical and mechanical stimulation are united, the reaction is given whether the chemical is edible or not; Pearl found it occurring in response to sodium carbonate (561).

Evidence of the influence of physiological condition upon the reactions of planarians is furnished by the fact that the resting planarian shows a decidedly lowered susceptibility to stimulation. Bardeen found that if the animal was not

already in motion, it gave no positive response to food in its neighborhood (20).

§ 18. *The Chemical Sense in Annelids*

In our own experience, as has been said, the "food sense" is represented by the two senses, taste and smell, the stimulus for the one being fluid, and that for the other gaseous, so that the latter enables us to perceive objects at a distance. For water-dwelling animals, such as most of those whose behavior we have been describing, the distinction evidently cannot well be drawn. If such an animal perceives food at a distance, the stimulus is necessarily diffused through the water, and Lloyd Morgan has proposed the term "telæsthetic taste" for the sense which makes such perception possible (504, p. 256). The term indicates that this sense corresponds to taste in an air-dwelling animal because the stimulus is fluid, but differs in that it allows perception of a distant object, as taste in the ordinary sense does not. In the most familiar representative of the Annelida or segmented worms, the common earthworm, as in the land planarian, a distinction analogous to that between smell and taste in our own sensory experience may be made; in the leeches and marine annelids it cannot.

Gentle and continuous mechanical stimulation produces in the earthworm "positive thigmotaxis"; that is, the animals have a tendency to crawl and lie along the surface of solids (686). That there is some discrimination of edible from inedible substances when in contact with the body Darwin thought probable from the apparent preference of the worm for certain kinds of food (171). In the earthworm *Allolobophora fætida* we find a differentiated response to contact and chemical stimulation. These worms live

in barnyard manure. When placed on scraps of shredded filter paper moistened with water they refuse to burrow; when the filter paper is wet with a decoction of the manure they burrow as soon as they come into contact with it. The adequate stimulus for burrowing is thus a combined mechanical and chemical one; the chemical stimulus **alone** is insufficient, for filter paper thus prepared has no **effect** on the worms unless they are actually in contact with it (686). Using the human terms, the case is one of taste rather than smell. Nagel suggests that the earthworm's chief use for a chemical sense is to help it find the moisture which is necessary to its life (522); but curiously enough *Allolobophora fatida* seems to have no power of doing this from a distance. Smith found that a worm would crawl around a wet spot on paper until its skin dried, without crawling into it. If by accident it happened to touch the moist place, it would enter and remain there (686). Parker and Parshley (555) find that the head end of the worm is negatively stimulated by contact with a dry surface, and will withdraw soon after such contact. There seems no satisfactory evidence that worms respond to chemical stimulation from a distance by positive reactions, although Darwin believed that they found buried food by "the sense of smell" (171). Chemical stimuli not in contact with the body do produce negative reactions (522), but these reactions do not differ from the responses to strong mechanical stimulation. They are of various forms—turning aside, withdrawing into the burrow if the tail is already inserted, squirming, and so on, the differences being correlated with differences in the intensity and location of the stimulus and in the excitability (physiological condition) of the animal. But nothing in the character of the response suggests that negative reaction

to a chemical stimulus has a different conscious accompaniment from that of negative response to a mechanical stimulus. The most natural interpretation of them all on the psychic side is that of unpleasantness, increasing in intensity as the reaction takes a more violent form.¹ The *time occupied in reacting* has, however, been made a basis for differentiating the response to different chemicals. It was found that if the worms were suspended by threads, and their anterior ends dipped into solutions of sodium, ammonium, lithium, and potassium chlorides, the animals reacted to these substances with diminishing promptness in the order just given. The differences in reaction time were marked. Now all four of these substances produce in man nearly the same taste quality, salt, for which the common constituent chlorine is therefore held responsible. The sodium, lithium, ammonium, and potassium ions have apparently but little effect on the human taste organs. Since the earthworm reacts with decided time differences to the four, it may be that its taste organs are specifically affected by each, and that different taste qualities may be occasioned in its consciousness, supposing it to be conscious (554). Kribs (410) has obtained evidence of localized chemical sensibility in the annelid *Æolosoma*; weak chemicals would produce a reaction only if applied to the sensory hairs of the head end. Leeches

¹ W. W. Norman argued that the squirming reactions of worms, and the corresponding reactions of other animals to injurious stimulation, cannot be taken as evidence of an accompaniment of disagreeable consciousness, because of the fact that when the worm, for instance, is cut in two, the squirming movements are confined to the posterior piece, while the head end crawls away undisturbed. The head end, he urges, containing the cerebral ganglia, ought to be the part capable of suffering, but it gives no reaction (525). We cannot, however, conclude from the absence of a reaction under abnormal conditions that when it occurs in the normal state it has no conscious accompaniment.

seem to be excited to their feeding reaction by a combination of mechanical and chemical stimulation. They are very sensitive to slight water disturbances, and react by stopping the respiratory movements if a needle is touched to the surface of the water above them. Food juice diffused through the water makes them very active; while in this state they will attach themselves to a glass rod, but drop off at once. When they attach themselves to food substance, however, they hold on with traditional tenacity. Chemicals of various kinds produce withdrawing reactions, and Löhner (438) finds evidence that leeches experience "taste compensation." When we have to eat sour fruit we cancel the sour sensation by putting sugar on the fruit. A five per cent. sugar solution produced withdrawing reactions in a leech, but if the sugar solution was mixed with a nine per cent. salt solution, its strength had to be raised to seven and five tenths per cent. before the leech reacted to it.

§ 19. *The Chemical Sense in Mollusks*

In the case of the Mollusca there is little satisfactory evidence on the subject of the chemical sense. The Acephala, to which the clam, oyster, and scallop belong, do not take food by active movements; hence, of course, they can have no specific feeding reactions. Chemical sensibility, distributed over the surface of the body, has been observed in lamellibranchs, a branch of the Acephala (522). Gasteropods, including snails and slugs, have, owing to their active food taking, more use for a chemical sense; in marine snails it seems rather definitely localized in the feelers (522). Yung found in the snail *Helix pomatia* that smell was most acute at the end of the feelers, but that the animal even when deprived of its

feelers could distinguish perfume. Taste he found best developed near the lips, and touch sensibility distributed over the body, but especially toward the end of the feelers (834, 835).

Of two freshwater snails, *Physa* and *Lymnæa*, the latter, whose movements are slower, can sense food at a greater distance than the former. In *Physa* an interesting relation between the chemical and mechanical stimulation produced by contact with food is apparent. "If *Physa*," says Dawson (177), "was moving at a moderately rapid rate when it came in contact with the meat, it received a sufficiently strong stimulus to cause it to turn away, to pause and then turn back. It would seem that the mechanical stimulus was not only sensed first but obeyed, and then the chemical stimulus was in turn sensed and obeyed." The limpets *Patella* and *Calyptraea* respond to the neighborhood of non-irritating oils by withdrawing reactions (583). Irritating chemicals, of course, are not proper olfactory stimuli, but one can hardly be sure that a stimulus which like oil of bergamot would be non-irritating to the human mucous membrane, is non-irritating also to the body surface of an animal. Mollusks in general seem to have chemical sensitivity distributed all over the body surface, although certain regions are especially sensitive. Piéron (585) finds in marine snails three modes of chemical excitability: an aerial distance excitability, on all parts of the body with predominance of the mouth, the anterior edge of the foot, and the siphon; a contact sensibility in both air and water, on the mouth, the horns, and probably elsewhere; and a delicate distance sensibility in the water, located in the regions of the mouth, the horns, the anterior edge of the foot, and the osphradial region.

§ 20. *The Chemical Sense in Echinoderms*

In the phylum of the echinoderms, under which are classed starfish and sea-urchins, the "circular symmetry" of body structure characteristic of the coelenterates reappears. Starfish were found by Romanes many years ago to show, besides pronounced negative reactions to strong or injurious mechanical stimulation, what he called a sense of smell. Its manifestations depended on the *physiological condition* of the animal; that is, upon its degree of hunger. If kept several days without food, a starfish would immediately perceive its presence and crawl toward it. "Moreover, if a small piece of the food were held in a pair of forceps and gently withdrawn as the starfish approached it, the animal could be led about the floor of the tank in any direction." By cutting off various parts of the rays, Romanes found that "the olfactory sense was equally distributed throughout their length"; and he also showed that the ventral and not the dorsal surface of the body was concerned, by varnishing the latter, which left the reactions unaffected, and by observing that when a bit of food was placed on the back it remained unnoticed (642, pp. 321-322). Preyer reported great individual differences in the responses of starfish to food stimulation; while certain specimens were unmoved by the neighborhood of food, an individual of another species came from more than six inches away and fell upon it (617). Whether the unlikeness of behavior was due to the species difference or to a difference in the degree of hunger does not appear. In the holothurian *Thyone briareus* feeding movements could not be produced by external stimuli, and apparently result from the internal state of hunger (565).

§ 21. *The Chemical Sense in Crustacea*

The highest invertebrate animals belong to the phylum of the Arthropoda, like the annelid worms in their segmented structure, but more highly organized in many respects. The body of a typical arthropod consists of a series of segments, one behind another, each segment with a pair of appendages. The higher an arthropod stands in the scale, the more modification and differentiation of function there is in the segments and appendages; the former often become consolidated, and the latter become modified for swimming, walking, or sensory purposes. The lowest grand division of the Arthropoda is that of the Crustacea.

As the animals of this group are covered with a hard outside shell, sensitiveness to touch and chemical stimulation is ordinarily referred to certain hairs scattered over the body, and to the modified appendages of the anterior segments which we commonly know as "feelers," the large and small antennæ. That mechanical contact stimuli in certain Crustacea give rise to specialized reactions is evidenced by observations on the hermit crab. This animal, as is well known, has acquired the instinct of taking up its abode in empty shells, most commonly those of some gasteropod mollusk. When wandering about in search of a dwelling, the crab's reactions to the objects it meets show adaptation to the character of the stimulus, for it will not investigate a glass tube or ball; the smooth surface seems not to be the adequate stimulus for beginning the movements involved in exploring and entering a shell (194).

The responses of Crustacea to food stimulation vary, as might be expected, with different genera and species. Nagel finds the rôle of the food sense in aquatic Crustacea very insignificant; they occasionally show antennal move-

ments in the presence of food, he says, but are not guided to it (522). That general restlessness is shown by various Crustacea in the neighborhood of food, but not in contact with it, has been observed by Bell in the crayfish (40), by Holmes in the amphipod *Amphithoe longimana* (329), by Bateson in shrimps and prawns (24), and by Bethe in the green crab (49). Bethe arranged a series of aquaria one above the other, with a connection between them, and found that when food was placed in the uppermost compartment the crabs in the lower ones were successively excited as the food juices diffused themselves from each compartment to the one below. In the amphipod *Amphithoe longimana*, the small antennæ and the mouth parts appeared to be the regions especially sensitive to food stimulation; if the food touched one of the former, the animal instantly made a dart for it. Touching the antennule with a needle very rarely caused such a reaction (329). Bateson's shrimps and prawns had their food sensibility located chiefly in the antennules, though if food was placed very near them they would show disturbance even when deprived of antennules (24). Balss (15) finds the sense of smell in the shrimp *Palæmon* located in the antennæ, and also in other parts; taste in the mouth parts and tips of the thoracic legs. This was the case also with Holmes's amphipod. Bell, on the other hand, found the whole body of the crayfish sensitive to chemical stimulation, and no evidence that the small antennæ were especially concerned. The crayfish's reactions to contact with food were such as to direct the stimulus toward the mouth; negative reactions of rubbing, scratching, and pulling at the affected part were obtained by stimulation with acids, salts, and other irritants (41). Chidester (120) found that the crayfish would go to freshly cut meat more quickly than to meat whose surface had had

time to dry. Evidences of irritation by the neighborhood of asafœtida were observed also by Graber in *Pagurus* (268).

In some Crustacea the sense of smell is possibly concerned in guiding the male to the female. Certain copepods which daily migrate from near the surface of the water to greater depths and back again have had this behavior explained as a result of the reactions of the females to light, plus the tendency of the males to follow the females. That the latter is an affair of chemical stimulation is indicated by the fact that the females were sought even when concealed in tubes (534). In the case of some other Crustacea, however, the sexes do not seem to be aware of each other's neighborhood until they come into actual contact (331, 333).

§ 22. *The Chemical Sense in Arachnida*

The two most important divisions of the phylum Arthropoda, besides the Crustacea, are those of the Arachnida and Insecta. Spiders, as is well known, have highly developed responses to mechanical stimulation; the web-making species in particular are sensitive to very slight web vibrations. The food reactions of spiders have never, so far as the writer knows, been tested, but various observers report sensitiveness to chemical stimulations, such as those produced by odorous oils, not in contact with the body. Spiders of the family Attidæ would react to glass rods dipped in such oils and brought close behind them, but would not react to clean glass rods when similarly placed (570). The reactions seem to be of a negative character (618), and, of course, in all such cases it remains uncertain whether the possible conscious accompaniment is a specifically olfactory unpleasantness or an unpleasant irritation of the body surface. Pritchett found that irritating and

non-irritating oils gave negative reactions (618); but an oil that belongs, for us, to the latter class might belong to the former in the case of a spider. If the sensibility were sharply localized, that fact would point in the direction of a specific olfactory sensation; but while some authorities think the spider's feelers or palpi are smell organs (47), others believe that sensibility to chemical stimulation is distributed over the body (452, 618). Nagel finds no specific organ of smell and little smell sensibility in spiders (522).

A member of the Arachnida which presents but slight superficial resemblance to the spiders is *Limulus*, the horseshoe crab. *Limulus* shows taste reactions, but no response to smell stimuli. If the mandibles at the base of the legs be rubbed with inedible objects, there is no reaction. Similar negative results are obtained by holding strong-smelling food close to the mouth or jaws. But if an edible substance be rubbed on the mandibles, strong chewing movements take place. Ammonia or acid vapor will produce these same chewing reflexes, but the claws make snapping movements "as though to pick away some disagreeable object." If a wad of blotting paper wet with ammonia or acid be laid on the mandibles, the chewing movements are reversed and the object is sometimes picked up by the claws and removed. Patten found organs which he believed to be gustatory on both the mandibles and the claws (557). Pearl observed no gustatory reactions in the free-swimming embryo of *Limulus* (562).

§ 23. *The Chemical Sense in Insects*

Throughout all the branches of the animal kingdom thus far mentioned, the chemical sense has functioned chiefly as

a food sense. There has been but little evidence of the development of qualitative discrimination within the sense itself. That is, while in many cases an animal can apparently distinguish the edible from the inedible, and gives negative reactions to irritating chemicals, one would hardly be justified in saying that it possesses more than one food sensation quality; while in our own case, of course, though we make comparatively little use of the sense of smell, the qualitative discriminations possible by its means are many. But we come now to a group of animals where there appears a remarkable development of qualitative variety in the sensations resulting from chemical stimulation; namely, the Insecta. As the reactions of animals to mechanical stimulation, on the other hand, offer evidence of little qualitative difference in the accompanying sensations, we shall give but slight attention to them in what follows.

To begin with, there is evidence that taste and smell are distinct in many insects. The water beetle *Dytiscus marginalis*, found apparently unresponsive to food at a distance, will bite with especial eagerness at filter paper soaked in what Nagel calls "a pleasant solution" (522). Ants fed honey mixed with strychnin will taste it and then stop, and will do this even when the antennæ and mouth palpi are removed, indicating that the taste organs are in the mouth itself (231). Similar results have been obtained from similar tests on wasps, and it has been observed that wasps so treated will hesitate when offered pure honey afterward (786).

Essenberg (208) found that the water strider, when offered flies which had been soaked, some in quinin and alcohol, some in coal oil, some in ammonia, approached them "carefully," left them, and then returned and devoured

them, a proceeding which proved fatal in certain instances. *The insects would stop and retreat just before reaching a drop of coal oil.*

Vitus Graber tested the reactions of various insects to odors by the method which we called on page 55 the Method of Preference. This was Graber's favorite mode of studying the effect of stimuli upon animals. Applied to olfactory stimuli it consisted in offering a choice between different compartments, containing each a different odor. The animal's power of discrimination was argued from the tendency to choose certain odors rather than others. Such preferences were shown by the insects (268). The method, however, as was noted above, is unsatisfactory, because discrimination might exist where preference did not. Another criticism urged against Graber's experiments is that the odors used were too strong and irritating. There is always the possibility that such substances affect other nerves than those of smell. The insects observed by Graber displayed choice between odors even when their antennæ were removed. There is much evidence to show that the antennæ are the true organs of smell in insects. Various flies and beetles which are in the habit of laying their eggs in putrefying flesh will not react to it when their antennæ are removed, and it has been shown that insects which seem to find their mates by response to olfactory stimulation fail to do so when deprived of antennæ (231). Interesting "compensatory movements" have been seen in silkworm moths with one antenna removed; they turned, that is, in the direction of the remaining antenna (397). We shall note movements of this class later in insects with one eye blackened, and in fish with one auditory nerve cut. The exploring movements of the antennæ which certain insects make in seeking a proper place to

lay their eggs have been taken as evidence of the smell function of these organs (574). McIndoo (455, 456, 457, 458), however, has recently presented evidence against the olfactory function of the antennæ. His experiments were performed on beetles, ants, honey bees, and hornets. His line of argument is as follows. While it is true that insects whose antennæ have been removed fail to respond normally to odors, this is because such insects are abnormal in all their behavior. There exist in various regions of the body of insects, as for instance the bases of the wings and legs, small pores containing sense cells; these McIndoo calls olfactory pores. He finds by measuring the time required for insects to respond to odors, that this reaction time is lengthened more decidedly when the olfactory pores are varnished over than when the antennæ are removed.

The function of the chemical sense in the mating processes of insects is one of the most remarkable phenomena connected with the sensory reactions of animals. Forel says he had a female *Saturnia* moth shut up in his city room, and that within a short time a number of males came and beat against the window (231). Riley hatched in Chicago some moths from the *Ailanthus* silkworm, which were carefully confined. No other specimens were known to exist within hundreds of miles. A virgin female was put in a wicker cage on an *ailanthus* tree, and a male, with a silk thread tied around the abdomen for identification, was liberated a mile and a half away. The next morning the two were together (637).

The most interesting observations on the sense of smell as used in the mating of insects, however, are those of Fabre. A cocoon of the "*Bombyx du chêne*," a species of which Fabre had not seen a specimen in the locality for

twenty years, was brought to him, and from it a female hatched. Sixty males sought her within a few hours after she reached maturity. Fabre noticed in this and other cases that shutting the female in an air-tight box prevented the males from being guided to her, but that the smallest opening was enough to allow the odor to escape; that the males were not in the least confused or led astray by placing dishes of odorous substances about, and that they would seek anything on which the female had rested for a time, a fact which suggests that the stimulus is a secretion of the body, as it is known to be in silkworm moths. Fabre offers the suggestion that smell stimuli as they are operative in the animal kingdom generally may be of two classes: (1) substances which give off particles in vapor or gas, and (2) substances which give off a form of vibration. Our own olfactory sense is limited to the first class of stimuli, but some animals, notably insects, may be sensitive to both (216). Certainly the marvellous sensitiveness involved in these mating reactions suggests a kind of response to stimulation unknown in human experience.

§ 24. *How Ants Find Food*

In many ways the Hymenoptera are the most interesting of insects, particularly those members of the order which have developed community life. Their reactions to chemical stimulation have been the subject of a large mass of literature, some of the more important results of which we may now undertake to survey, considering ants, bees, and wasps successively. Sir John Lubbock was among the earliest observers to indicate the great importance of chemical stimuli in the life of ants. In the first place, he demonstrated that it is by chemical stimulation that

ants are able to follow each other to supplies of food; or to larvæ, for an ant's behavior to an ant larva found in the course of its wandering is like its behavior to food; the larva is picked up and carried to the nest. Lubbock put some larvæ on a glass plate at a little distance from one of his artificial ant nests, and set a similar empty plate beside it; he then made a bridge of a strip of paper leading from the nest toward the plates, and connected each of them with this bridge by a separate short paper strip. He placed a marked ant at the larvæ; she picked up one and returned to the nest. She soon appeared followed by several others; when she had reached the larvæ, and before the others had arrived at the dividing of the ways, Lubbock exchanged the short strips, so that the one over which the marked ant had passed now led to the empty plate. The following ants all took this path, indicating that they were guided by some trace which her footsteps had left. Lubbock was inclined to think, however, that some kind of communication must have passed between the marked ant and her fellows in the nest to induce them to follow her, and also that this communication might on occasion convey some notion of the quantity of food or larvæ to be had. He placed three glass plates near an ant nest, connecting each of them with the nest by means of a paper strip. On one plate he put a heap of several hundred larvæ, on the second two or three only; the third was empty. He put a marked ant on each of the plates, and captured all the ants which they led back with them. Many more ants came to the plate with the larger heap of larvæ than to the others. Lubbock explained this by supposing that the ant from that dish had in some way communicated to the nest the greater numbers at her disposal (441, pp. 172 ff.). Obviously it would be enough to suppose that the smell of food or

larvæ about an ant returning laden to the nest is a stimulus to her nest mates to follow her; that this smell is stronger, the larger the stock she has found, and hence acts as a more powerful stimulus. The question arises, however, as to how an ant can distinguish between the smell of food or larvæ on an ant that has just found a store of either, and the smell of the food and larvæ in the nest, which must adhere to all her nest mates. Some peculiarity of behavior on the part of the foraging ant would seem to be needed if she is to induce her fellows to accompany her to food. Wheeler, whose knowledge of ants is unsurpassed, but who is perhaps a little too much inclined to humanize them, says (783, page 535), "I believe that no one who has watched ants continuously and under a variety of conditions will doubt that they actually communicate with one another. This is clearly indicated by the rapidity with which they congregate on a spot where one of their number has found food, or retire from any spot in which a few of their number have been killed or injured." Such communication, whatever its nature, concerns us here only so far as smell may be involved in responding to it.

§ 25. *The Use of Smell in Path-finding by Ants*

The homing of ants is a puzzling problem. Bethe (51) thinks that ants, as reflex machines, are drawn along the path back to the nest by the chemical stimulus deposited on the path by their own bodies. Piéron (579) has maintained that in some species we have to do with a kind of muscular memory, the ants simply reversing, on the homeward path, all the turnings they took on the way out, like a top unwinding itself. Cornetz (143, 144, 145) claims for ants the mysterious power of registering in their bodies

the general direction of their outward course and reversing it when they have found a load to be carried home. We may consider very briefly the facts that have been brought to the support of these various hypotheses. There are really two problems involved in the homing of ants. There is, first, the problem of the homing of a solitary forager, who, having found food at the end often of a very long and rambling course, is able to get back to the nest. Secondly, there is the problem of the nature of a frequented ant road, along which many ants constantly travel to and from the nest. The evidence that smell functions in the homing process is strongest in the case of such a frequented trail. Lubbock's experiments showed that on these trails the recognition of visual landmarks plays no important part. For instance, he placed larvæ in a dish on a table connected by a bridge with an ant nest. He accustomed the ants to go back and forth between the dish and the nest by a path which he diversified with artificial scenery, such as rows of bricks along either side, and a paper tunnel. When the path was thoroughly learned, he moved the bricks and the tunnel so that they led in a different direction: the ants, however, were not at all disconcerted by this cataclysm of nature, but followed the same track as before, evidently guided by their own footprints (441, p. 259). Forel (233) showed that when a piece of wood is laid across a well-frequented path of certain species of ants, they are much disturbed and at a loss to follow the trail, and Bethe (51) reports that drawing a finger across the trail will apparently break its effectiveness as a guide. That the chemical deposited by the ants is volatile he concludes from the following observation. If a strip of paper be placed across an ant path, the ants on coming to it stop, quest about, and are delayed until one accidentally runs across the strip

and others follow. The piece of paper is thus gradually adopted into the ant road; if it is subsequently removed, the ants stop and are bewildered at the place where it was, showing that the earlier traces of their footsteps, under the paper, have evaporated. Again, Bethe thinks he has evidence that the chemical stimulus left by the feet of ants going from the nest is different from that deposited by those going to the nest, and that ants on the way home will not follow a track made by the feet of other ants on the outward journey, and *vice versa* (51). Bethe found that when the usual road to an ant nest had been interrupted by the removal of a heap of sand, and the road across the breach had been established solely by incoming ants, the outgoing ants refused to follow it, and made a new road for themselves (51). Wasmann thinks this may have been done merely on account of the faintness of the recently established path as compared with the old one (762). Bethe observed also that if a strip of paper had been adopted into an ant road, and was then, while an ant was on it, rotated through 180 degrees, the ant stopped and was disturbed on coming to the end of it (51). Experiments on rotating ants were made also by Lubbock (441), and seem to give puzzling and conflicting results; it is not clear why, even on the assumption that there is a difference in odor between the road to the nest and that from the nest, an ant on a road which led both ways should have found her course interrupted by rotation. One fact, Bethe thinks, shows that even assuming two road smells is not enough. Ants of certain families (*Lasius*) which habitually make regular and frequented roads can, if they come upon one of these roads in wandering, at once take the proper direction, either to or from the nest. Evidently the mere presence of two smells would not enable them to do this.

Bethe suggests that the particles of the two chemical substances are also differently polarized, so that one of them can be followed only in one direction, the other in the opposite direction (51)*. Wasmann objects to this that an ant returning on its own traces would destroy them, as the opposite polarizations would cancel; and that similar confusion would occur on a narrow and much frequented road (762). He and Forel (233) both think that, granting the discrimination between the outward and inward paths, which is made by only a few families of ants, the direction is most probably given by a perception obtained through the antennæ, of the "smell form" of the footsteps. Since the antennæ are movable organs, like the hands, they may well, Forel suggests, mediate spatial perceptions of the form and size of odorous patches. This hypothesis would fall to the ground if McIndoo's contention that the antennæ are not smell organs were sustained.

On the whole, there is much evidence indicating that smell plays an important part in determining the response of ants to well-frequented roads. We may now consider the case of the solitary forager. Santschi (654) believes that he has seen a smell trail "intentionally" deposited by an ant, dragging her abdomen along the path. Bethe, whose general position that ants, and indeed all invertebrate animals, are reflex machines requires him to avoid any hypothesis that would involve learning or memory on the part of these animals, is of course anxious to explain the homing of the solitary foraging ant as a smell reflex. He placed near the entrance of a nest a large sheet of paper covered with lampblack, on which the footsteps of the ants could be traced. On this paper he put a supply of food. When an ant had found the food, Bethe reports that in returning to the nest she always followed the path by which she had

come, except that when the original path had crossed itself in loops, the ant omitted the loops in her homeward way (51). Apparently, however, many species of ants do not thus retrace their own footsteps. The "muscular memory" theory of Piéron (579) is based on the observation that if a homing ant be carefully lifted and deposited at a little distance away, she will continue her course until she has traversed a distance equal to that which she would have had to go to reach her nest, if her course had not been interrupted. Cornetz's theory (143, 144, 145), that an ant has some mysterious power of retaining an impression of the direction in which she set out, and of reversing this direction when she is ready to return home, is derived from a long series of very careful field studies. He reports that a foraging ant takes a certain general direction and makes excursions to right and left in search of food. When the food has been discovered, she reverses her original direction, but does not actually retrace any part of her outgoing path. Piéron (591) is impressed by these observations, and inclined to think that a mysterious factor is actually involved. That the direction of the light may serve as a guide in the homing of ants is indicated by observations of Lubbock (441), Turner (722 a), and Santschi (654), but the ability of ants to find their way about in the dark is sufficient proof that it cannot be the sole factor.

§ 26. *How Ants "Recognize" Nest Mates*

Another problem of ant life to which smell appears to furnish the key is that of the *recognition of nest mates*. It has long been known that an ant entering a strange nest, though of the same species, is likely to meet with rough treatment, and even be put to death. Now Forel

found in 1886 that ants of the genus *Myrmica* whose antennæ were removed would attack their own nest mates (231). It seems probable that each nest of ants has a peculiar odor which is the basis of the distinction between friends and foes. Bethe tested the smell theory by dipping an ant first in weak alcohol, then in water, and then in the juices obtained by crushing the bodies of a number of ants of another species. He found that an ant thus treated would be attacked and killed by its own nest mates, but could be introduced, though not so easily, into the nest whose odor it now presumably bore, even though its appearance was quite different from that of the ants therein (51). Wasmann repeated these experiments with much less success than Bethe; bathing *Myrmica* ants with essence of *Tetramorium* ant did not preserve them from final destruction at the jaws of the latter, though it delayed their fate; nor did much bathing with foreign nest odors induce the ants to attack beetles of the species *Lomechusa strumosa*, their accustomed "guests" in the nest, though they seemed disturbed at first. Wasmann apparently thinks other factors besides smell, vision perhaps, enter into the recognition process (762). Bethe, in a later paper, suggests that Wasmann's negative results may have been due to the fact that the nest smell very quickly returns to the ants after it has been removed; he himself took account only of the first reaction of other ants toward the one subjected to treatment (52). Piéron (581 a) has repeated Bethe's experiments and confirmed his results with eighteen different combinations of ant species. Many factors, however, modify the hostile reaction to foreigners. Piéron finds that certain species are inclined to be tolerant. Attacks are more frequent near the nest than at a distance from it. A solitary ant tends to run away rather than to

attack. Males do not distinguish strangers from nest mates, and a female after the marriage flight will be received in a strange nest. Brun (104) has observed that ants carrying larvæ will be tolerantly received, and that if ants from two nests are tumbled into a sack together and then tumbled out into a strange place, their hostility to each other is inhibited by their general disturbance and fright.

Termites, which, although they belong to the order of neuropterous insects and not to the Hymenoptera, have developed an organized community life much like that of ants, show the same tendency as ants to attack strangers. The young are not attacked, nor does the fighting response occur when large numbers are hastily tumbled together. That the hostile response is made to a chemical stimulus, at least in part, appears from the fact that "a well-washed termite is attacked by both aliens and fellows," but the observations do not give quite so definite results as those on ants (6).

Fielde, as the result of a study of the genus *Stenammas*, concludes that each ant is the bearer of three distinct odors: the individual odor, which enables her to follow her own trail in a labyrinth, and the reception of which depends upon the tenth segment of the antennæ; the race odor, dependent on the eleventh segment; and the nest odor, dependent on the twelfth (219). No other investigator, however, finds evidence of any such specialization of the antennal segments, and McIndoo, as we have seen, wholly rejects the antennæ as a smell organ. In a later article Fielde concludes that the nest odor of the worker ants is derived from their queen mother; that the odor of the queen is unchanging, and is imparted to her eggs. The worker, however, gradually changes its odor. Queens of diverse

odors may be produced by the influence of males that are the offspring of worker mothers and have the differentiated worker odor. A young ant isolated from the pupa stage until many days old will single out its queen mother from queens of other species, but will show decided suspicion of older sister worker ants. A mixed nest formed of newly hatched ants of different species was separated for seven months. On rejoining each other, the ants showed hostility; their odor, Fielde argues, had changed. But young ants of one species were received by those of the other species. Fielde does not hesitate to introduce the psychic factor and say that the latter remembered the odor of the young ones, having been associated with it in their own youth. The suggestion might be made that the young ants had not as yet developed any specific odor, but this is opposed by the observation that newly hatched *Lasius* ants from a strange colony were not received by a nest of *Stenammus*, while young *Lasius* ants from a colony with which the *Stenammus* had been acquainted in youth were accepted eleven months after the latter had been segregated. It is an affair of the memory, Fielde is assured; and she says, "If an ant's experience be narrow, it will quarrel with many, while acquaintance with a great number of ant odors will cause it to live peaceably with ants of diverse lineage, provided the odors characterizing such lineage and age environ it at its hatching" (224). Bethe held that an ant's own nest odor offered no stimulus to it at all, but that fighting reflexes were occasioned by any foreign nest odor (51). Many facts, however, seem to tell against this view; among others, the early observation of Forel that a *Myrmica* ant deprived of its antennæ attacks everything in sight (231). It should, according to Bethe's theory, live peaceably with all.

Thus we see that in spite of some divergence of testimony, there is evidence that ants have a variety of qualitatively different smell experiences: the smell of food and of larvæ, probably distinct, though there is no experimental proof of the fact; the individual smell of an ant's own footsteps; a possible distinction, in some species, between the smell of the outgoing and that of the incoming paths; and the different odors which seem to be responsible for the discrimination between nest mates and foreigners. If it were true, as Fielde maintains, that loss of the eighth and ninth segments of the antennæ renders an ant incapable of caring for the young, then the recognition of larvæ and pupæ would depend upon a specific odor (219).

§ 27. *How Bees are Attracted to Flowers*

In bees the sense of smell is equally well developed. But no topic in comparative psychology has been more hotly disputed than the use which bees make of this sense, and the extent to which they depend, rather, upon sight. Darwin (170) and H. Müller (512, 513) thought both color and fragrance influential in attracting insects to flowers. Plateau maintains that the chief influence guiding bees to flowers is smell, and that color has little effect. He made a number of experiments in which the brightly colored corollas of flowers were cut off without disturbing the nectaries, and claims to have found that the visits of bees to the mutilated flowers were as frequent as before (600-603, 605). On the other hand, Giltay obtained opposite results; the flowers whose corollas were removed were neglected by bees, while those which were covered so as to be invisible but not so as to prevent the odor from escaping, were also unnoticed (259). Josephine Wéry found that the propor-

tion of bees visiting flowers with intact corollas to those visiting flowers with the corollas removed was 66:18 (778). Kienitz-Gerloff criticises Plateau's figures and the accuracy of his experiments (400). Forel found that a bee with the antennæ and all the mouth parts removed, hence probably incapable of smell, returned to flowers for honey, though of course without success (231). Andreæ thinks that among diurnal insects those which live on the ground, and take but short flights, are more influenced by smell; while the freely flying insects are attracted by the sight of flowers (5). On the whole, inconspicuous flowers are more often fertilized by wind than by the visits of insects.

§ 28. *How Bees Find the Hive*

Most complicated of all is the problem as to how bees find their way back to the hive. It is obvious that the simple method of following a chemical trail is ruled out for insects that fly. Bethe abandons the puzzle as insoluble (51). Von Buttel-Reepen attempts at length, and with a vast amount of apic lore, to refute his position. It would be impossible to give more than the briefest statement of the arguments of both sides. Bethe maintains that the smell of the hive does not guide the bees back to it, because he found that if the hive were rotated slowly enough to allow the cloud of nest smell at the opening to move with the opening, the bees returning would not follow it for more than 45°, but would go to the place where the opening had been. He thinks they are not guided by sight, because when he completely changed the appearance of the hive, masking it with branches and other coverings, the bees were not disconcerted, but flew straight to the mouth of the hive. He brings other evidence against the vision

hypothesis which we shall discuss in Chapter XI. An *unknown force, he concludes, guides the bee in its homing flight* (51). Von Buttel-Reepen believes that visual memory will explain all the facts; that the bees were not disturbed by the altered appearance of their hive because they knew their way so thoroughly that nothing could disturb them by the time they had come so nearly home. The visual memory required is, he admits of a peculiar sort, which we shall consider in a later chapter. The odor of the hive does coöperate with vision in certain cases; when a stock of bees has been moved without their knowledge, they fly out without making any "orienting flight," as they commonly do on leaving a new place, a fact that is one of the evidences for the visual memory theory. Nevertheless, many of them succeed in finding their way back, and then, if their hive is placed among a number of others, von Buttel-Reepen thinks they "smell" their way back to the right one. He mocks at Bethe's unknown force, on the ground that it must sometimes lead the bee to the hive and sometimes back to the place where food has been found (115). Bethe attempts to answer this by saying that the force acts in coöperation with the physiological condition of the animal; the laden bee follows it to the hive, the bee with the empty crop is led back to the food supply (52). Of course one may say what one pleases about the *modus operandi* of an unknown force without fear of disproof, but also without carrying much conviction.

That a mysterious sense of direction exists in the bee is concluded by Bonnier (97) from the following evidence. He first showed that bees whose eyes had been covered by pigmented collodion could go directly to their hive if they were not more than three kilometers away. Smell, however, or muscular memory, might account for this.

He then attempted to demonstrate that smell was not an essential factor in guiding bees. He placed two stands carrying honey, one 200 meters, the other six meters from the hive, and marked the bees that visited each stand, proving that a given bee almost never went to both, but continued to visit the stand where it had first found honey. Here, however, sight might have been the determining influence. Wagner (751) thinks that bees in the neighborhood of the hive are influenced by visual landmarks, but that in their longer flights they depend on a sense of direction, which seems however to be a form of visual memory. On the whole, smell would appear to be only one factor, and not a very important one, in guiding the flights of bees.

§ 29. *How Bees "Recognize" Nest Mates*

The nest smell, which characterizes each hive and prevents the reception of strangers, who are treated precisely as by ants in similar circumstances, is composed according to von Buttel-Reepen of the following odors: the individual odor of different workers; the family odor, common to all the offspring of the same queen; the larval smell and food smell; the drone smell, the wax smell, and the honey smell. There are various ways in which the mode of reaction to a foreign nest smell is modified. If two bee stocks are placed side by side, and one has the queen and entire brood removed, it will go over to the other stock and be kindly received. One can understand that the attraction of the queen and brood odor may overcome the tendency of the foreign nest smell to repel the invaders, but it is harder to see why the more fortunate stock should allow itself to be invaded. Further, a bee laden with honey can get itself received by a foreign stock that has exchanged

hives with it, where an unladen bee is attacked; here the smell of the honey may overcome the foreign smell. As is well known, two alien stocks may be united by sprinkling them with some odorous substance. The queen odor is the strongest factor in the nest smell; in swarming it *overcomes the tendency to return to the old nest*, and queenless swarms will join themselves to foreign swarms having a queen. The apparent attention paid to the queen while laying eggs, the gathering of workers around her trilling their antennæ toward her, suggest strongly that her odor is pleasant to them. The queen, herself, however, is perfectly indifferent to any foreign nest smell, and will beg food of any bee, even those which are angrily crowded around her cage in a foreign hive. Drones also will go from stock to stock, and are always peacefully received until drone-killing time begins. It has usually been supposed that the unrest displayed by a bee stock when deprived of its queen is due to the absence of the queen odor, and it seems almost certain that this must be a powerful influence, though von Buttel-Reepen thinks it is not the *only* influence, for he has observed that if the queen be replaced in the honey space, removed from the rest of the hive, the bees will quiet instantly, before the smell has had time to diffuse itself. Also, bees sometimes behave as if they had lost their queen when she is only put in a cage, and her odor is perfectly accessible (115).

It is clear that bees as well as ants are capable of distinguishing a considerable number of smell qualities. Probably the same thing is true of the social wasps. In the solitary wasps, however, we find less evidence of a highly developed sense of smell, or rather of a great variety of smell reactions, and the solitary bees are very likely less influenced by smell than the social bees. In the interesting study of

the solitary wasps by Mr. and Mrs. Peckham, it appears that sight plays a far more important rôle than smell for these insects, and the return to the nest in particular seems to be almost entirely an affair of sight (572, 573). In general, the greatest development of qualitative variety in the sense of smell is found in the social Hymenoptera, and is probably a product of the social state. Perris, however, noted that the solitary wasp *Dinetus* was much disturbed in finding its nest hole if he had placed his hand over the hole during the wasp's absence, and thought the odor of his hand was distracting to the insect (574).

§ 30. *The Chemical Sense in Vertebrates*

Although the vertebrates stand at the head of the animal kingdom, yet in point of complexity of structure and behavior the lowest vertebrate is far below the highest members of the invertebrate division. When we undertake to study the responses to special stimulation displayed by this same lowest vertebrate, the little *Amphioxus* or lancelet, it is like going back to the earthworm. The only kind of evidence that contact, chemical, and temperature stimuli produce specific sensation qualities is found in the fact that sensibility to them is differently localized, and may be independently fatigued. To weak acid, the head end of the animal is most sensitive, the posterior end less, the middle least; to contact with a camel's-hair brush, the two ends are equally sensitive and more so than the middle; to a current of warm water the order of sensitiveness is: head end, middle, posterior end (541).

For fishes, as for all aquatic animals, the distinction between smell and taste becomes obscure. The neighborhood of food not in actual contact with the body seems to stir

fish to activity, but not to direct their movements. Bateson (25) and Herrick (297) both obtained evidence of this; Nagel, on the other hand, declares that fish do not perceive food at a distance except by sight, and that the function of the first pair of cranial nerves in these animals must *remain uncertain* (522). *The well-developed character* of these "olfactory" nerves and lobes, whose function in higher vertebrates is certainly connected with smell, would argue against the supposition that smell can be wholly lacking in fishes. It is generally agreed that a contact food sense exists in fish; Nagel, however, holds that its organs are situated only about the mouth (522), while Herrick has good experimental proof that fishes which have "terminal buds," structures resembling taste buds, distributed over the skin, are also sensitive to food stimulation applied to different regions of the skin. He thinks that Nagel's negative results were due to the fact that instead of food stimuli in his experiments he used chemicals with which the fish would not normally be acquainted (297).

Parker (546), experimenting with catfish and the young of a species of lamprey, found the whole body surface more or less sensitive to salt, acid, and alkali; the body of the lampreys was sensitive also to quinin solution, but that of the catfish was not; neither animal displayed skin sensitiveness to sugar solution. Cutting the nerve supply to the olfactory organs, the lateral-line organs (see page 128), and the taste buds failed to abolish skin sensitiveness, which Parker therefore concludes must depend on free nerve endings in the skin. He distinguishes three forms of chemical sensibility in these lower vertebrates: common chemical sensibility, for which free nerve endings are the organ; taste, dependent on the taste buds; and smell, dependent on the olfactory nerves, and responding to much

more dilute solutions than the other two, thus being capable of acting as a distance sense (550). A number of species of fish have been shown to possess smell, by demonstrating that they can discriminate between small bags filled with food and similar bags stuffed with inedible substances, and that this discrimination is lost when the olfactory nerves are cut or the nostrils are closed (547, 142). Shelford and his associates (673) have thrown light on a very interesting problem in animal behavior, the migrations of fish. It is well known that salmon return to fresh water to spawn, ascending rivers, and that other fish perform migrations that are of great economic importance to the fishing industry. Shelford has demonstrated that fish are very sensitive to slight variations in the chemical constitution, the salinity, for instance, of the water in which they live, and their responses to such changes may well account for all their wanderings.

Among amphibians, the spotted newt seems to show a relation between smell and the "common chemical sense" not unlike that existing in fishes. The olfactory nerves seem to be required for the discrimination of food. When chemicals are applied to the body, the head end is much the most sensitive region, even when the olfactory nerves are cut. Acids and alkalies cause very marked reactions; salt is less effective and sugar not effective at all (629). Cole (135) studied the time required for the reflex withdrawal of the hind legs of leopard frogs when four chlorides, those of ammonium, potassium, sodium and lithium, were applied in solution. He found that the speed of reaction corresponded to the order in which these salts affect the human sense of taste. That a common chemical sense, and not pain, was involved in these skin reactions was indicated by the fact that they persisted when ordinary pain reactions,

to pricks, were abolished by cocaine. Risser (638) reports that while sight seems to be more important than smell in determining the mature toad's reactions to food, tadpoles failed to distinguish packets containing food when their nostrils were plugged. Immature *Amblystomas*, which in the normal condition react positively both to motionless food and to moving inedible objects, lost the first type of response when their nasal pits were removed, and the second type when their eyes were operated on (1112).

In birds sight and hearing are so well developed that the chemical sense assumes less importance. Birds seem to have a sense of taste: the chicks experimented on by Lloyd Morgan, for example, showed disgust on picking up bits of orange peel instead of yolk of egg (506, pp. 40-41). Herring gulls make similar manifestations on being fed salt fish, and take bread soaked in meat juice more readily than water-soaked bread (697). Raspail (626) thinks that birds abandon eggs which have been handled because they detect the fact by smell; that they find buried grubs by smell, and are guided by this sense to concealed food and water. The last statement he supports by the observation that their tracks lead straight to hidden food on their first visit to it, showing that it was not found by accident. Strong (696) made a careful study of the olfactory apparatus in twenty-seven of the thirty-five existing orders of birds. He concludes that "the olfactory organs of birds are of too great size to be set aside as non-functional," but that as one passes from the lower to the higher orders of birds there is a tendency towards retrogression in these organs. The crow family, sometimes considered to be the highest birds, show extremely minute smell organs. "The sense of smell has evidently been disappearing in birds with the great development of vision."

The hypothesis has been put forward by Cyon (165) that smell may somehow function in guiding the long flights of birds. Watson (770) found that the noddy tern could find its way from Key West to its nest on the Tortugas with the nostrils tightly sealed. Strong, however, points out that this bird has very small olfactory organs, and thinks it possible that other birds may make more use of the olfactory sense in homing and migrations. The fulmar, for instance, is a bird which makes very long ocean flights, and has an enormously developed olfactory apparatus. Strong (696) made experiments with the ring dove in which he was apparently able to establish some association between the smell of bergamot in a certain compartment and the choice of that compartment as containing food.

When we come to the Mammalia, we find in the great majority of types a very high development of qualitative discrimination in the sense of smell. Hunters know it to be the chief defensive weapon of wild animals, and it has retained great keenness in many domesticated ones, — the cat, for instance, which will be awakened from slumber in the garret by the odor, quite unsuspected of human nostrils, of some favorite food being prepared in the kitchen, and is thrown into ecstasy at a faint whiff of catnip. The dog, however, is the hero of this field of mental prowess. The experiments of Romanes on the power of a favorite setter to track his scent are well known. In one of them he collected a number of men, and told them to walk in Indian file, "each man taking care to place his feet in the footprints of his predecessor. In this procession, numbering twelve in all," Romanes says, "I took the lead, while the gamekeeper brought up the rear. When we had walked two hundred yards, I turned to the right, followed by five of

the men; and at the point where I had turned to the right, *the seventh man turned to the left, followed by all the remainder.* The two parties . . . having walked in opposite directions for a considerable distance, concealed themselves, and the bitch was put upon the common track of the whole party before the point of divergence. Following this common track with rapidity, she at first overshoot the point of divergence, but quickly recovering it, without any hesitation chose the track which turned to the right." It had previously been ascertained that she would not follow the scent of any other man in the party save her master, and failing him, the gamekeeper. "Yet . . . my footprints," continued Romanes, "in the common track were overlaid by eleven others, and in the track to the right by five others. Moreover, as it was the gamekeeper who brought up the rear, and as in the absence of my trail she would always follow his, the fact of his scent being, so to speak, uppermost in the series, was shown in no way to disconcert the animal following another familiar scent lowermost in the series" (644). Such behavior indicates not only that the dog can experience a variety of smell qualities, which is also the case with us human beings, but that it has the power to analyze a fusion of different odors and attend exclusively to one component, a power that we lack almost entirely. When we experience two smell stimuli at the same time, it is but rarely that we can detect both of the two qualities in the mixture; usually one of them swamps the other, or else a new odor unlike both results. But the dog, and probably many other animals, can analyze a smell fusion as a trained musician analyzes a chord. In this respect, if not in the variety of smell qualities, the olfactory sense has undergone degeneration in us, and so far as we can judge, the fact is due to the habit

of relying rather upon the sense of sight. Even in the case of the monkey, Kinnaman reports that the animals he was testing with regard to their power of discriminating the size, shape, and color of vessels in one of which food was placed, always looked, never smelled, for the food (401).

CHAPTER VI

SENSORY DISCRIMINATION: HEARING

§ 31. *Hearing in lower invertebrates*

THE sense of hearing, in all air-dwelling animals, is that sense whose adequate stimulus consists in air vibrations; for human beings these vibrations may reach a frequency of 50,000 (single vibrations) in one second and still produce an auditory sensation. But the meaning of the term "hearing" for water-dwelling animals, and hence for most of the lowest forms of animal life, is more difficult to determine. In the Protozoa it seems to have no meaning at all; the reactions of these animals to water vibrations are indistinguishable from their reactions to mechanical stimulation. But in some of the coelenterates the possibility of a specific auditory sensation quality has been suggested by the discovery of a peculiar sense organ. While varying in its structure in different genera and orders of coelenterate animals, this organ consists typically of a small sac, filled with fluid and containing one or more mineral bodies. Apparently these latter could operate in connection with a stimulus only when the stimulus was constituted by shaking the animal, or in some way disturbing its equilibrium. They might then serve as means for the reception of water vibrations, as the ear serves for the reception of air vibrations; they might, in short, be primitive organs of hearing. Accordingly the term "otocysts" was given to organs of this type wherever they were found in the animal

kingdom, and the mineral bodies in the otocysts were called otoliths.

But experiments upon coelenterates have entirely failed to show that animals of this class react to sounds (205, 741, 521). And in some coelenterates, as well as in higher animals having the same type of organ, the removal of the so-called otocysts has been found to involve disturbance of the animal's power to keep its balance and maintain a normal position. Hence Verworn has suggested that for "otocyst" and "otolith" the terms "statocyst" and "statolith" might appropriately be substituted (741). In jellyfish, indeed, even the balancing function of the statocyst organs appears doubtful; and it is possible that they function in response to shaking and jarring (514, 521). In any case, there is no evidence whatever of a specific auditory sensation in the consciousness, if such exists, of coelenterate animals.

Nor has any reaction to sound been demonstrated in either the flatworms or the annelid worms; their sensitiveness to vibrations seems to be an affair of mechanical stimulation. Darwin's experiments on this point are well known. The earthworms which he observed were quite insensitive to musical tones, but when the flower pots containing their burrows were placed on a piano, the worms retreated hastily as soon as a note was struck (171). Most observers agree that mollusks also react only to mechanical jars (e.g., 190), and that the statocyst organs found in some mollusks have no auditory function. Bateson, however, records that a certain lamellibranch, suspended by a thread in a tank, responded by shutting its shell when a sound was produced by rubbing a finger along the glass side of the tank (25). The echinoderms are apparently insensitive to auditory stimuli (617, 641).

§ 32. *Hearing in Crustacea*

In the Crustacea the function of the statocyst organs has been the subject of much dispute. They are in this group of animals sometimes closed sacs with statoliths, sometimes open sacs containing grains of sand. Most commonly the organs are situated in the basal segment of the small antennæ. There is usually inside the sac a projection bearing several ridges of hairs, graded in size, which tempt to the hypothesis that they respond to vibrations of different wave lengths, as the fibres of the basilar membrane of the human cochlea are supposed by the Helmholtz theory to do. Hensen, indeed, placing under the microscope the tail of a small shrimp, *Mysis*, whose statocyst is situated in that region, observed that the long hairs of the tail vibrated in response to musical tones, from which he infers that the statocyst hairs may do so¹ (294). In 1899 he was still inclined to believe that the latter can serve no other than an auditory function (295). Nevertheless the weight of authority is in favor of regarding the "sac" in Crustacea as a static rather than an auditory organ. The only evidence of sound reaction in two shrimp-like forms, *Palæmon* and *Palæmonetes*, was a "flight reflex" given by some individuals when sounds were produced very near them in the water; and although this response ceased when the statocysts were destroyed, the fact is of little significance, as other reflexes also were abolished by the operation (38). To sounds made by tapping the wall of the aquarium *Palæmonetes* reacted by leaping away from the wall nearest to it, even though the leap was made toward the

¹ This observation is sometimes incorrectly quoted as if the hairs concerned were actually the statocyst hairs. Cf., for example, Morgan, 504, p. 266.

sound. When both statocysts were removed, the reactions were still made, but not so markedly nor at so great a distance from the sound. A similar response to the striking of a partially submerged glass jar was seen in a decapod, *Virbius zostericola*, which has no statoliths (616). Mysis has been found to react to sounds when the statocysts are destroyed (48). The fiddler crab, which is amphibious, responds in water to vibrations by retreating slowly from the vibrating walls, and does the same when blinded and deprived of its statocysts, but gives no reaction when the antennæ and antennules are removed. On land these animals do not respond to sounds, only to vibrations produced in the earth, for instance by stamping (616). No sound reactions have been found in the crayfish (40). In short, such responses to vibrations as occur among the Crustacea seem affairs rather of mechanical than of true auditory stimulation; nevertheless Bethe (48) and Hensen (295) are both inclined to believe, as did Delage, who first called attention to the static function of the statocysts (180), that they may be auditory organs also. The "static sense" of Crustacea will be discussed later.

§ 33. *Hearing in Spiders*

In spiders the same difficulty arises, of deciding whether the reactions to sound are tactile or auditory. There are no statocysts, but the delicate hairs on the body and legs of the animal have been held to be auditory organs. Dahl, a number of years ago, found them responding to the tones of a violin (166, 167), but this test, which Hensen applied to Mysis, is of very doubtful significance; as Prentiss suggests, the hairs on the back of the human hand do the same (616). When various species of spiders were tested by holding

tuning forks near them or their webs, only the web-making species gave any response. These latter would not react to ordinary noises, nor to the sound of a small fork, but to the humming of a large fork they responded always by raising the front legs, and sometimes by dropping from their webs (570). Two Texan species that were experimented upon by placing them in a cage free from vibration gave no response whatever to tuning forks of various pitches or to other sounds (618). It seems, then, highly probable that spiders are sensitive only to vibrations communicated to their webs, and very likely these furnish tactile rather than specific auditory stimulation. The observation of Boys may be quoted: "On sounding an A fork, and lightly touching with it any leaf or other support of the web or any portion of the web itself, I found that the spider, if at the centre of the web, rapidly slews around so as to face the direction of the fork, feeling with its fore feet along which radial thread the vibration travels. Having become satisfied on this point, it next darts along that thread till it reaches either the fork itself or a junction of two or more threads, the right one of which it instantly determines as before. If the fork is not removed when the spider has arrived it seems to have the same charm as any fly, for the spider seizes it, embraces it, and runs about on the legs of the fork as often as it is made to sound, never seeming to learn by experience that other things may buzz besides its natural food. If the spider is not at the centre of the web at the time that the fork is applied, it cannot tell which way to go until it has been to the centre to ascertain which radial thread is vibrating." If, however, it has followed the fork to the edge of the web, and the fork is then withdrawn and brought near again, the spider reaches out in its direction. If the spider is at the centre of the web and a sounding fork is

brought near without touching the web, the spider does not reach for it, but drops down at the end of a thread. If the fork touches the web again, the spider climbs the thread and finds the spot very quickly (100).

§ 34. Hearing in Insects

The sense of hearing in insects also is problematical. When the insect makes a sound itself, which, as in the case of crickets, is connected with the mating process, it would seem *a priori* highly probable that it can hear. Various structures have been designated as auditory organs, the finely branched antennæ of mosquitos and gnats, on the same doubtful evidence that they have been found to vibrate in response to musical tones (479); and in the Orthoptera certain very peculiar structures situated on the front legs of grasshoppers and crickets, and in the first segment of the abdomen in locusts. These structures Graber called chordotonal organs, and he felt convinced from experimental tests that they were auditory. The cockroach, *Blatta*, while running about the room will stop, he says, for an instant when the strings of a violin are struck. A blinded specimen, hung by a thread, became violently agitated at a sudden tone from a violin. A water insect, *Corixa*, although undisturbed by the water vibrations produced by pushing a bone disk toward it in the water, gave decided reactions when the disk was connected with an electric bell. Other water beetles were still more sensitive. That they distinguished pitch differences Graber thought probable from the fact that he observed reactions of different degrees of violence to sounds of different pitch; and their discrimination of intensity changes he thought demonstrated by the fact that if a continuous tone, sounding while a water

beetle is swimming about, be made suddenly louder, the speed of the insect's movements visibly increases. It is going rather far, however, to pass from the evidence that insects discriminate sounds made by their own species from other sounds to the conclusion that "they like us have the capacity to analyze, at least to a certain degree, these peculiar clangs or noises, and to distinguish clearly from one another the partial tones that compose them" (264).

Tower thought that he had observed the potato beetle reacting to the sound of a tuning fork (717). Will noted responses from a male beetle to the stridulation of a female of its species enclosed in a box 15 cm. away (786). Rádl made the suggestion that the organs which Graber called chordotonal organs, and which contain a fibre stretched between two points of the integument, represent a kind of transition between "*Gemeingefühl*" and hearing. In support he offers the following evidence: the fibres resemble the tendons in which some muscles end, and are very likely developed from tendons; the organs exist in insects that have no use for hearing, such as grubs shut up in fruits; insects have not been shown to respond to pure tones, but only to noises, such as the cricket's chirping, which for us affect *Gemeingefühl*. Further, there is no evidence that hearing ever guides insects to each other; in short, it is but a rudimentary sense, and its organs are those which serve also to register muscular activity. It is, in insects, a "refined muscular sense" (624). Regen (630) demonstrated very prettily an apparently auditory reaction in the female cricket. He placed in the centre of a wide area on the floor two glass vessels, one lined with black paper, the other transparent. In the opaque vessel he placed a chirping male; in the transparent vessel a quiet male.

Normal females ran to the vessel which contained the chirping male, but ignored the other vessel: females whose "tympanal organs" on the forelegs had been operated on did not react to either vessel. That the response was not to an odor liberated by the movement of the male's wings in chirping, was shown by removing the edges of the wings, so that their motion, while otherwise unchanged, was noiseless: the response of the females ceased.

It seems likely that the auditory sense, if it exists in insects, would be confined to those which produce sounds, and its qualities limited within the range of such sounds. Turner (731), however, finds that silkworm moths, alighted on hanging shelves and thus protected from jarring, respond by waving their wings when an organ pipe, a pitch pipe, and various notes on the Galton whistle are sounded. One species, which failed to respond, he rendered more excitable by rough handling, and then succeeded in stimulating the sound reactions. Several different species of *Catocala* moths were found to respond to high notes on the Galton whistle, either by flying or by quivering their wings. By touching the insect at the moment when the tone was sounded, thus giving it a "life significance" to the insect, some of the moths were trained to react to a lower organ tone (256 vibrations) even when they were not touched. These moths are not known to make sounds (733). Most species of ants produce no sound that the human ear, even with the aid of a microphone (441), can detect, although certain East Indian species are reported to make a loud hissing noise when disturbed (760), and some American species are said to chirp (202, 782). Ch. Janet maintains that ants of the *Myrmicidæ* make a stridulating noise (357, 358). The weight of evidence

is also against the existence of sound reactions in ants; careful experiments by Fielde and Parker on a number of species led to the conclusion that the only vibrations responded to were those which were communicated through the solid on which the ants stood, and received through the legs (226). It is probable that the observers who have come to opposite conclusions have not in every case been careful to exclude the possibility of such vibration of the substratum. Wasmann, for instance, thinks he has seen reactions to sound; he noted that ants in an artificial nest raised their antennæ and lifted the fore part of their bodies when he scratched with a needle on some sealing wax with which the nest had been mended (759). He also quotes Forel's account (230) of a species which makes an "alarm signal" by striking the ground with its abdomen: this, remarks Wasmann naïvely, must be perceived by the ants, "otherwise it would not be an alarm signal"! (760). If perceived, it may of course be as a tactile rather than an auditory sensation. Weld has observed reactions to the sound of whistles and tuning forks in several species of ants, and even concludes that they perceive the direction from which sounds come; but since, of the four observations upon which this latter opinion is based, two were cases where the ants hurried toward the sound and the others cases where they backed away from it, the possibility of mere coincidence seems not to be excluded (776).

As regards the auditory sense in bees, there is again a difference of opinion. They do, of course, make sounds, and sounds of different quality, under different conditions. Yet Lubbock entirely failed to get bees to respond to any kind of sounds artificially produced (441), while Bethe urges that the sounds produced by bees are involuntary, like the

sounds of our own breathing and heart-beats, and that there is no more evidence that bees can hear them than that we can hear these sounds in our own case (52). Forel is positive that insects in general cannot hear (231). Von Buttel-Reepen, on the other hand, who knows bees thoroughly, thinks that the sense of hearing plays a considerable part in their life. He believes that the disturbance produced by the loss of a queen is communicated to the whole hive by the peculiar wailing noise made by some members and instinctively imitated by the others, and that this disturbance is calmed by a similar dissemination of the "happy humming" produced on her restoration — hearing playing a more important part than smell. The starting of a swarm, he thinks, is also largely a matter of sound communication. The process begins by the coming out of certain bees which push in among the bees hanging at the entrance of the hive and stir them up to swarming by making sounds. The "swarm-tone" is peculiar and often disturbs the inhabitants of neighboring hives that are not ready to swarm. Also, a swarm can be guided to a new dwelling if a few bees are taken there; they call the others by loud humming. If during this process the new hive is moved, the bees will go on for a few moments, in the direction in which they started, then slowly turn, guided by the tone. A few may keep on in the original direction. We may look with suspicion, however, upon von Buttel-Reepen's suggestion that these latter, having passed beyond hearing of the call, are guided by the recollection of the tone they heard at first! He refers also to the shrill noise made by the young queens ready to swarm, and to the peculiar uneasiness produced when a strange queen is being attacked, and resulting, he thinks, from her "cries of pain" (115).

§ 35. *Hearing in Fishes*

Throughout the vertebrate animals there exist structures bearing analogy to our own ears, whose function might therefore be supposed to be auditory. But in the lowest vertebrates the only structures of the human ear represented are the semicircular canals, and these suggest a static rather than an auditory organ. The cyclostomes, eel-like and semiparasitic forms classed below the true fishes, have a pair of sacs one on either side of the head, containing mineral bodies, and each leading into one or two semicircular canals. In the true fishes the sac has two chambers, marked off from each other by a constriction. Three semicircular canals open from the foremost chamber, two lying in the vertical plane, and one in the horizontal plane. The chambers contain "statoliths" and fluid.

That the semicircular canals in fishes have a static¹ function has been shown by experiments to be described later. Is the fish ear also an organ of hearing? Again authorities disagree, and it is probable that species differ. Kreidl got no response from goldfish when vibrating rods were placed either in the water or in the air near the water. Only when the fish were made more sensitive by strychnin did they react, and only to noise, not to tone. They reacted quite as well, moreover, when the ears were removed; whence it was concluded that their sensitiveness to noise resided in the skin (408, 409). A similar negative conclusion regarding auditory sensation has been reached by F. S. Lee (416), by O. Körner as a result of experiments on twenty-five species (404), and by Marage (460 a), using

¹ The word "static" is here used to mean "relating to equilibrium" in general, not to static equilibrium as distinguished from dynamic equilibrium.

vowel sounds sung on notes ranging from C₂ to G₆, transmitted through rubber tubes, the tests being made on eight species. On the other hand, Bigelow found that the goldfish on which he experimented were sensitive in their normal condition, but insensitive when the auditory nerves were cut, and thinks that Kreidl's operation did not remove the whole of the fish's ear (54). Triplett thought both perch and goldfish were excited by the sound of whistling, which usually preceded their being fed (720). Parker tested the killifish, a species of minnow, using the sustained slow vibrations (40 complete swings per second) of a bass viol string placed on one side of the aquarium as a sounding board. The fish cage was suspended in the aquarium from an independent support. Normal fish responded to the vibrations, usually by movements of the fin, 96 per cent. of the time. Fish in which the nerves to the ears had been cut responded in 18 per cent. of the tests; those in which the skin had been made insensitive, but the ears left, in 94 per cent. Since causing the string to vibrate jarred the whole aquarium somewhat, these experiments were checked by others where the stimulus was produced by placing the stem of a vibrating tuning fork against the sounding board. The results were the same as in the first set of tests. Parker concludes that the ears of the minnow are certainly organs for the reception of sound; but as he obtained no such reactions from dogfish, he is inclined to think that different species vary (535, 536). In later experiments (544) on the dogfish, Parker finds that individuals with the "auditory" or eighth nerve cut show diminished sensitiveness to the blow of a pendulum, the force of whose impact on the walls of the aquarium could be measured, while cutting the optic nerve or cocainizing the skin has no effect on the responses to these stimuli: his conclusion is that the reactions are

auditory. In the squeteague (542), he infers from the results of operation that one part of the ear, the utriculus, functions in the maintenance of equilibrium, while the other part, the sacculus, is the organ of hearing. The otoliths, or statoliths, in the ears of the squeteague and dogfish Parker thinks have actually an auditory function, contrary to what is known of their use in invertebrate animals; when they were removed from the ear of the dogfish, he reports, there was no disturbance of equilibrium, but a reduction in the reaction to blows on the aquarium wall, and when the large otolith in the sacculus of the squeteague was pinned down, a similar result was obtained. Most sounds made in the air are extremely faint under water, but to sounds really propagated through water, Parker thinks many fish are sensitive. Certain sounds may actually attract them: the squeteague, for instance, itself makes sounds which may serve to bring the sexes together. Tests by Zenneck on *Leuciscus rutilus*, *L. dobula*, and *Alburnus lucidus* also led to the conviction that these fish, at least, could hear. A bell was struck by electricity under water, and occasionally a piece of leather was placed upon it at the point where the clapper struck. In the latter case the mechanical vibrations produced were, it was held, the same as those occasioned by the actual ringing of the bell, but the sound vibrations were destroyed. The fish reacted by swimming instantly away from the neighborhood of the bell when it was rung, but not when the leather was used; hence, apparently, they reacted to sound (840). These experiments, however, have been repeated on trout and eels by Bernoulli (43) with negative results.

Widely distributed among fishes is a curious set of structures known as the lateral-line canals. Along each side of

the fish. extending from head to tail, there is a row of pores opening into a long canal, which at the head divides into three branches, one going upward above the eye, a second below the eye, and a third down toward the lower jaw. The functions of these canals have given rise to much discussion among zoölogists, an exhaustive history of which will be found in Parker's monograph entitled "The Function of the Lateral-line Organs in Fishes." Parker first proved experimentally that the canals played no part in responses to the following stimuli: light, heat, salinity of the water, food, oxygen dissolved in the water, carbon dioxide, foulness of the water, hydrostatic pressure, steady currents flowing through the water, and sound. When, however, the water in the aquarium was made to vibrate slowly, about six times per second, the fish made certain characteristic reactions, differing somewhat for the four or five species observed, but always failing to appear when the lateral-line nerve was cut. Parker concludes that "the stimulus for the lateral-line organs (a water vibration of low frequency) is a physical stimulus intermediate in character between that effective for the skin (deforming pressure of solids, currents, etc.) and that for the ear (vibrations of high frequency), and indicates that these organs hold an intermediate place between the two sets of sense organs named" (539). The ear is thus regarded as actually derived from the lateral-line canal, as this in turn was derived from the skin. We may suppose that at least three different sensation qualities result from stimulation of the skin, the canals, and the ear, where hearing can be shown to exist.

Hofer (326 a) criticizes these experiments on the ground that when Parker cut the lateral-line nerves he also destroyed the nerves supplying the skin of the head, a partic-

ularly sensitive region to touch stimuli. It is, according to Hofer, the skin nerves that are affected by the slow vibrations which Parker thought to be the proper stimulus for the lateral-line organs, and in certain cases he demonstrated that such stimuli were responded to when the lateral-line organs had been destroyed. The true function of the lateral-line organs Hofer finds to be that of response to streaming movements in the water. A skin sensitiveness to currents would be of the greatest practical value in guiding the fish's migrations.

§ 36. *Hearing in Amphibia*

Emergence from the water, on the part of adult Amphibia, is accompanied by *disappearance of the lateral-line canals*, and consequently of whatever sensations these mediate. In the frog, the ear has a tympanic membrane lying at the surface of the head. A single bone, the *columella*, with one end against this membrane, lies across the middle ear. The internal ear is not essentially different in structure from that of the fish; there is no cochlea. Yerkes has made an interesting study of the reaction of frogs to sound. He found that they occasionally "straightened up and raised the head as if listening" when other frogs croaked or made a splash by jumping into the water. To no other sound did he get any apparent response, nor was it possible to make frogs in their native habitat jump or show any uneasiness by producing any sort of noise, so long as the experimenter remained invisible. "Apparently," Yerkes says, "they depend almost entirely upon vision for the avoidance of dangers." It is of course highly improbable that an organ should be adapted only to the reception of the croaking of other frogs and the splash of water, and not to noises made

in imitation of these; and Yerkes suggests that the frogs may hear many sounds to which they respond by inhibiting movement as a measure of safety. This view is confirmed by the results of experiments where the breathing movements of the frog's throat were registered by means of a lever resting against it and recording on smoked paper. Evidence from change of the breathing rate was obtained of the hearing of sounds ranging from fifty to one thousand single vibrations a second (807). Later, it was shown that sounds, although they did not, when given alone, cause the frogs to react, modified the responses to other stimuli, reinforcing or inhibiting them according to the interval between the sound and the other stimulus. This effect was noticed both when the frogs were in the air and when they were under water. It was more marked in the spring (the mating season) than in the winter. That it concerned the special auditory sense-apparatus, and hence may have been accompanied by true auditory sensations, was shown by the fact that it disappeared when the auditory nerves were cut. Sounds ranging from fifty to ten thousand single vibrations a second were effective (817, 815). This, of course, does not mean that the frog perceives such sounds as differing in pitch.

§ 37. *Hearing in Higher Vertebrates*

The reptilian ear does not differ markedly from that of amphibians. The writer knows of no experiments upon the sense of hearing in reptiles. The cochlea, the organ of hearing in mammals, is still imperfectly developed in birds. But if we grant that animals which produce sounds are capable of hearing them, some birds at least must be able to make pitch discriminations of wide range and great acuteness. The powers of imitation so

often evidenced in bird song are proof that this is the case.¹ Craig (157, 158) has carefully observed the social significance of a great variety of sounds made by pigeons, but gets little evidence that these birds learn new sounds by imitation.

Extremely significant are Hunter's (353, 354) experiments on the hearing ability of the white rat. Their net result is that these animals can hear only noises, not tones. None of the rats he tested was able to hear a tuning fork tone; the evidence is that they were unable, under the stimulus of both punishment and reward, to learn to turn to the right when the tone was sounded and to the left when it was not sounded. They could perfectly well acquire such a habit when the noise of clapping the hands was substituted for the tone. They could not form the habit when two forks of different pitch were sounded together as a signal to turn to the right. They acquired the habit of making the proper response when the tones of a whistle were substituted for the fork tones, but it was clear that they were really responding to the noise of the rush of air through the whistle, for they would react equally well when this noise was substituted for the actual blowing of the whistle. Moreover, they broke down in their choices when the whistle was sounded in another room, although they were not disturbed by the mere diminution of intensity in the sound of the whistle sounded near at hand; the natural inference is that removing the whistle to a distance made the noise accompanying its tone inaudible. In short, there seemed to be, for these rats, no difference between the sound of a pure tone and entire silence. Confirmatory results appear in

¹ Interesting evidence of this power in a bird which might not have been supposed to possess it was obtained by Conradi, who found that English sparrows reared by canaries acquired recognizable bits of the canary song (141).

Barber's (19) experiments on the white rat's ability to localize sounds: noises, such as those made by tapping on wood, were localized within an average limit of error of from two to four inches, but tuning-fork and organ-pipe tones were wholly ignored.

The experiments of Johnson (384) on the dog's ability to discriminate tones and noises gave results very similar to these of Hunter on the rat, and furnish an illuminating commentary on certain difficulties in experimentation on animals. Zeliony (839), working by the salivary reflex method described on page 57, had reached the conclusion that the dog can discriminate between tones whose pitch differs by only a quarter of a tone. Kalischer (388), whose interest lay in testing the work of Munk¹ on the localization of the central terminations of the sensory pathways for tone in the temporal region of the cortex, succeeded in training dogs, with and without temporal lobes, to snap for food when one tone was sounded and inhibit reaction when a tone of considerably different pitch was given. Rothmann (646 a) and Swift (699) also observed discrimination of tones in the dog, and Kalischer (388) claims for the dog memory of absolute pitch. But the experiments of all these investigators, including those who used Pawlow's method, suffer from the fatal defect that the experimenter was in the room with the animal tested, and hence might have presented other clues, by making slight involuntary movements, which could act instead of the tones to guide the animal's choices. How serious this objection is appears from Johnson's own results. His dog subjects all learned to discriminate between a tone of 256 double vibrations and one of 384 double vibrations, an interval of a fifth, whether the tones were sounded on tuning forks or on a wind appara-

¹ Munk, H., 1890. *Ueber die Funktion der Grosshirnrinde*. Berlin.

tus (the Stern tone variator); and to discriminate between a chord containing one of these tones and a chord containing the other tone. This was when the experimenter remained in the room. Experiments by a much more accurate apparatus, where electrically driven forks were sounded from another room, while the experimenter observed the dog also from an adjoining room, the tones being sounded with exactly the same duration, gave precisely opposite results: the dogs could not discriminate. (The test of discrimination was learning to turn to the right when one tone was sounded and to the left when the other tone was sounded.) Moreover, they could not even learn to take one turning when a tone was given and the other when no tone at all was given; apparently if they heard the tone at all they paid no attention to it. On the other hand, the noises of two electric buzzers, of different intensity, pitch, and timbre, were readily discriminated and localized by the dogs.

The same objection, that secondary clues derived from the presence of the operator may account for the seeming discrimination of sounds, applies to the work of Shepherd on cats (677, 678) and raccoons (676). The apparent fact that certain mammals are deaf to tones, while perfectly able to hear noises may, as Johnson suggests, be connected with the fact that even human beings cannot localize pure tones with any accuracy: a sound stimulus, to have practical significance, must be capable of being localized. Zeliony (839) trained a cat to come from one room into another when a C' whistle was blown, and thought he had evidence of the cat's ability to distinguish the sound of this whistle from that of others differing not more than a half-tone; but the difference reacted to may have been in the accompanying noises. Hahn (282) finds the bat very sensitive to high-pitched sounds, but not to low ones.

CHAPTER VII

SENSORY DISCRIMINATION: VISION

§ 38. *Change of Light Intensity as a Stimulus*

IN this chapter we shall omit all references to the function of vision as a spatial sense, that is, as giving rise to perceptions of form, size, distances, and direction.

It appears that light may act upon living beings either as a continuous or as an interrupted stimulus. That is, light maintained steadily at a constant intensity produces responses in organisms, and there are also reactions when the intensity of the light is suddenly altered, in the direction either of brightening or of darkening. Most physical forces act as stimuli only when they change in some way: an unchanging environment fails to call forth response. We may briefly survey the facts which point to the existence in animals of reactions to changes in light intensity.

Among the Protozoa, *Amœba*, when subjected to sudden changes in light intensity, checks its movement at the point where the light falls. This is just what happens when a mechanical stimulus is applied, and offers no evidence of a specific light sensation (378). Similarly, various ciliate and flagellate Protozoa give their ordinary negative or avoiding reaction to changes in light intensity; some of them make it on passing from a region of less to one of greater illumination, and thus "seek" the darker regions, while others give it when undergoing a change in the reverse direction, and thus tend to remain in lighter regions.

But if nothing distinguishes the negative reaction to photic stimuli from the negative reaction to any other stimulus, then nothing shows the existence of a sensation quality peculiar to the effect of light — *unless* a special receptive apparatus can be demonstrated. In a flagellate Protozoön called *Euglena*, a pigment spot exists near the anterior end. Now although pigment apparently is not, as Hesse (323) has emphasized, a necessary constituent of visual organs, yet its occurrence always suggests some relation to light, as it is essentially a kind of matter having the property of absorbing light. *Euglena* gives the negative reaction on entering a shadow. Is its pigment spot really an "eye spot" and concerned in this response? Apparently the reaction occurs before the pigment spot has entered the shadow, and as soon as the transparent tip lying in front of the pigment spot has been pushed into the shaded region (204). It is uncertain, then, what the function of the pigment spot is. But in another organism, which is structurally intermediate between the single-celled and the many-celled forms, pigment spots do play a rôle in light reactions. This organism is called *Volvox*, and it is really a colony of globular flagellates, each with its flagellum turned outward, and each with an "eye spot." Very weak light has no effect on the movements of *Volvox*; moderate light causes movement toward the source of light, and very strong light causes movement away from the source (332). Accurate observation of these movements indicates that the eye spots are essential to them; each individual responds to a change of illumination of its eye spot (464). This much evidence, then, we have that if *Volvox* possesses consciousness, changes of light intensity produce in it a specific sensation.

Among coelenterates, response to changes of light in-

tensity is found, although in the hydroid colonies of *Tubularia* it appears to be wholly lacking (564). Many sea-anemones are wholly unaffected by light stimulation, *Sagartia luciae* and *Metridium*, for example (286). Many others have been observed to contract when the light intensity is increased (266, 374, 521). *Eloactis producta* expands its tentacles only in light of low intensity, taking about fifteen minutes to do so when covered with a hood, and retracting in five minutes when the light is restored. This retraction is decidedly slower than that produced by mechanical stimulation (286); thus we have some evidence that it is accompanied by a specific sensation quality. That the responses to light are more marked in animals which have been living in comparative darkness than in those taken from illuminated spots, has been shown both for sea-anemones and for *Hydra* (228).

Many *Medusæ* or jellyfish also react to light more slowly than to other forms of stimulation. It is true that on *Sarsia*, a form tested by Romanes many years ago, light seemed to act as quickly as any other stimulus. If a flash of light were allowed to fall on the animal while it was moving about, "prolonged swimming movements" ensued; if it was at rest, it gave only a single contraction — another instance of the effect of physiological condition upon reaction. Sudden darkening produced no reaction, whence Romanes concluded that "it is the light *per se* and not the sudden nature of the transition from darkness to light which in the former experiment acted as the stimulus." There are, however, as we shall see, other animals in which an increase of illumination brings about response where a decrease fails, and *vice versa*. When a beam of light was thrown into a bell-jar containing many *Sarsiæ* and placed in a dark room, "they crowded into the path of the beam

and were most numerous at that side of the jar which was nearest the light." "There can thus," concludes Romanes, "be no doubt about Sarsia possessing a visual sense" (641, p. 41). But as these reactions are not differentiated in any way, they cannot be taken as evidence of a specific sense, unless indeed they depend on a specialized sensory structure. This latter Romanes found to be the case; Sarsia has pigment spots on the margin of its bell, and its response to light ceased when these were destroyed. Tiaropsis, another jellyfish studied by the same observer, gave further evidence of "a visual sense" in the fact that it responded to light more slowly than to mechanical stimulation. In Gonionemus, both difference in reaction time and dependence of response on a special organ indicate that light may produce a specific sensation, always granting the presence of consciousness. Yerkes found that this jellyfish, unlike Sarsia, reacts in the same manner in passing either from sunlight to shadow or the reverse. In both cases it stops swimming and sinks to the bottom. A sudden change of illumination, therefore, checks its activity. On the other hand, if when the light falls upon it the animal is at rest, it becomes active again; but sudden decrease of illumination has no effect upon the resting animal. The inhibitory effect of strong light falling upon the jellyfish while in motion Yerkes explains as a special adaptation. For one case of such increase of illumination occurs when the animal swims, bell upward, to the surface on being disturbed; the light of the surface is of course normally stronger than that in the lower regions. The inhibition of activity resulting causes the animal, after turning over, to sink slowly, bell downward, with expanded tentacles. This is a position that gives it a better chance of catching food and carrying it to the lips than is offered

by the right-side-up posture, where food would have to be carried downward against the upward current occasioned by the sinking of the animal. Light is not the only factor in producing the inversion at the surface, however, for it will occur in darkness. When swimming, *Gonionemus* moves toward the light if the latter is fairly intense, but comes to rest in the shaded portions of the vessel containing it. The reaction time to light is much slower than that to other stimuli, but the animal responds most promptly when certain pigmented bodies at the base of the tentacles are exposed to the stimulus. If the margin of the bell containing these bodies is cut off, no reaction to light can be obtained (802, 809, 825). A great variety of structures apparently sensory in function is found on the bell margin of different genera and species of *Medusæ*. Some of them are statocysts. Others suggest a visual function, and in the *Cubomedusæ* there are fairly well developed eyes.

Various annelids show response to changes in light intensity, the leech *Clepsine*, for example: the slightest shadow cast on the surface of the water in a dish where these animals are resting quietly will cause them to reach up and sway from side to side in an apparent search for prey (785). On the other hand Gee (256) says of the leech *Dina microstoma* that the casting of a shadow on it makes it contract. This is apparently the more primitive and the more common type of response to a change in light intensity. *Dina* contracts in just the same way when mechanically jarred, but a difference in the physiological process involved is indicated by the fact that these leeches get used to repeated shadows, and cease to respond, much more quickly than they get used to repeated jars. When the earthworm has partially emerged from its burrow, and has its tail still inserted, a flash of light will produce

quick withdrawal into the burrow (171, 327), but the reaction time to light is much longer than that to mechanical stimulation. The part of the earthworm's body affected by the light also influences the reaction. Darwin indeed reported that the worms withdrew into their burrows only when light fell on the head end (171), but decapitated worms were found by Graber to respond to light like normal ones, only less strikingly (266), and Yung (833) obtained evidence that sensitiveness to light is distributed over the body. According to Hesse the anterior end of the worm is most sensitive, the tail next, and the middle region least (316). Not only the region, but the amount of body surface affected, makes a difference. When the whole length of the worm was illuminated, the percentage of reactions was to that obtained where the front third only was involved as 26 to 10.2, while the relative occurrence of responses where the middle third and the posterior third alone were stimulated is represented by the figures 2.4 and 1 respectively (552).

In many of the marine worms well-developed eyes exist, although not such as are capable of giving clear images. Their function seems to be chiefly that of receiving stimuli from shadows. Many tube-dwelling worms will withdraw into their tubes if a shadow is cast upon them (285, 321, 650).

Turning to the molluscs, we find that the siphons of the Acepala, which are projected from the shell to take in currents of water containing nourishment, are withdrawn in response to sudden darkening in some cases, to sudden illumination in others, and in still other instances to either (195, 520, 650). The danger of arguing the existence of sensory discrimination from structure alone is well shown in the case of snails, for although many of them have eyes

of some degree of development, these very species have been shown to be devoid of sensitiveness to light (836, 837).

"Skioptic" reactions, or reactions to shadows, appear among various echinoderms. The sea-urchin *Centrostephanus longispinus*, for instance, which lacks even a rudimentary eye spot, will when a sudden shadow falls upon it direct its spines towards the shaded side. The reaction time involved is decidedly longer than that to mechanical stimulation, and moreover, although pieces of the animal will react to the latter, responses to shadows depend on keeping the system of radial nerves intact. (This observation, according to Cowles (155), does not hold for the sea-urchin *Toxopneustes*.) Hence Von Uexküll, who made the above observations, concluded that a special set of nerve fibres is concerned in photic reactions (735).

Dubois had suggested from studies on the mollusc *Pholas dactylus*, that in such cases the pigment changes which occur, under the influence of light, over the surface of the body, furnish the stimulus (195), but Von Uexküll thinks this impossible, as the light reactions occur before the pigment changes do. This migratory pigment, he believes, acts merely as a screen; the source of excitation for the optic fibres may lie in another pigment which he has extracted and found very sensitive to light (735). *Centrostephanus*, according to Hess (313), shows pigment changes when the light is decreased by a very slight amount, just enough to be perceptible to the human eye.

Starfish have pigment or eye spots on the arm-tips. As a rule, they seek light: Romanes (641) and Tiedemann (710) report that the light reactions are abolished if the eye spots are removed. MacCurdy (453) finds, however, that in *Asterias forbesii* the light reactions are independent of eye spots: Cowles (156) has shown that *Echinaster* will

react to light without eye spots, although some evidence of dependence on the sense organ is indicated by the fact that the response is slower; Plessner (607) holds that skin sensitiveness is responsible for reactions to light intensity, and that the eye spots enable the animal to respond to the direction of the light; Cowles (155), again, observes that when pieces of starfish and sea urchins are cut off, their tentacles and suckers still move in response to the casting of a shadow.

Among crustacea, which are provided with a peculiar visual organ, the compound eye, to be described later, the chief function of the eye seems to be that of responding to shadows and movements. Bateson, watching shrimps and prawns, noted that they apparently could not see their food when it had been taken from them and lay near at hand, but quickly raised their antennae when an object was passed between them and the light (24). The little fairy shrimp, *Branchipus*, will stop swimming as soon as the edge of a shadow falls upon it. Skioptic reactions in the family of Cirripedia, to which the barnacles belong, were noted by Pouchet and Joubert in 1875, as well as the fact that those individuals which were attached to rocks, where a sudden shadow might mean danger, reacted, while those attached to floating objects, and therefore normally exposed to light fluctuations, did not (615).

When we come to animals with well-developed eyes, the specialized response to changes in light intensity gives place to reactions involving the use of a more or less adequate image of the stimulus object. But as we have seen, the most primitive type of reaction to a sudden change of light intensity is the checking or inhibiting of the animal's movements. This type of reaction is called by Loeb "*sensibility to difference*." In many cases its relative

slowness, as compared with similar reactions to other stimuli, or its dependence on a special organ or region of the body, give evidence that it is accompanied by a specific sensation quality.

§ 39. *The Continuous Action of Light: Photokinesis*

When light stimulates not through its change of intensity, but through its action as a constant force, its effects are apparently of two kinds. One of these is the phenomenon which Loeb (433) calls the tropism, from the Greek word meaning "to turn." In the tropism, the organism takes up a definite position with reference to the action of a force. The phenomenon is therefore connected rather with the spatial aspect of the sense of sight than with its qualitative aspect, and we shall consider it in a later chapter. The other type of effect caused by light as a constant stimulus is that it stimulates or inhibits the general activities of the animal. Thus some animals are restless in strong light, others in darkness. As a result of this influence, the former tend to form collections in the dark, where they remain quietly; the latter in the light. This influence of a certain intensity of light to stimulate to activity we may call its *kinetic* effect, or *photokinesis*. The coelenterate Hydra, for example, has a disposition to come to rest in the more illuminated parts of the vessel containing it (719, 791). Very strong light, however, makes it wander about until it happens to reach a more shaded region. Thus if the animal is subjected to light either above or below a certain "optimum" of intensity, it is restless. A vague uneasiness is the kind of psychic accompaniment to this behavior most naturally suggested. Since repeated strong mechanical stimulation also will make the animal wander, nothing

points to the existence of a specific visual quality in this consciousness.

The medusa *Gonionemus* is less active in darkness than in light, and comes to rest in darkened regions, where it thus tends to collect (802). Such collections are evidently not due to a definite choice on an animal's part.

On the planarian, the general effect of light stimulation is *kinetic*; it comes to rest in the shaded portions of a vessel (20, 425, 429, 317). Decapitated and hence eyeless planarians respond to light, but their reactions are delayed (432); thus there is a certain amount of dependence on the visual organ.

Photokinetic effects seem to be common among insects, many of which, the house fly, for example, and the mason wasp (728), are active in light and sluggish in darkness. These animals are naturally so much more active than *Hydra* and planarians that we do not find them forming collections in the regions where they can rest; they seem able to continue in rapid motion for long periods, and it is rather a pleasurable than an uneasy activity that is suggested by the aërial dances of insects in the sun.

§ 40. *The Problem of Visual Qualities: Invertebrates*

It is a well-known fact that when a human being with normal vision looks at the band of spectral colors, the band appears brightest to him in the region of the yellow. Yellow rays, that is, produce most effect on the normal human retina. They are also the most intense rays in sunlight. Now if a totally color-blind human being looks at the spectrum, he sees it as a band of different grays, the brightest gray being not in the yellow region but in the yellow-green; that is, it has been shifted towards the

violet end. He also sees in place of the red a gray darker than the brightness of red to the normal eye would lead one to expect. This altered distribution of brightness in the spectrum occurs for the normal eye also, under very faint illumination: in twilight the spectrum looks to the normal eye just as it does to the totally color-blind eye, a band of grays brightest in the yellow-green region. If we had no other means of deciding whether or not a man was color-blind, we should take as evidence of color-blindness the fact that for him the brightest region of the spectrum lay in the yellow-green rather than the yellow, in ordinarily bright light. It is therefore of some importance to the problem of color vision in the lower animals to find *how strongly* the light rays of various wave-lengths affect them. But we must bear in mind that for the lower animals it is impossible to conclude color-blindness from the fact that the brightness values, that is, the effective intensities, of the different colors are what they would be for a color-blind human being. Just this unsafe inference is, however, drawn by certain authorities.

In plants, the maximum effect of colored light is exerted by the rays at the violet end: violet, indigo, or blue. The problem has been investigated for microscopic animals by an arrangement such that two beams of light fall on the organism at right angles to each other. Now if the organism has a tendency either to seek or to avoid light, and if the two beams are of equal intensity, the animal will move on a diagonal between the two beams. If either ray has a stronger effect than the other, the course of an animal which seeks light will be inclined towards the more effective beam; that of an animal which avoids light, towards the less effective beam. If the two beams are of different colors, it will thus be possible to test the stimu-

lating efficiency of differently colored rays. Mast (474), using this method, found that some animal forms, such as the larvæ of the blowfly, are most strongly stimulated by that region of the spectrum which acts most strongly on the color-blind human being; others, such as the earthworm and the larvæ of the worm *Arenicola*, were most responsive to blue, as plants are. We shall later note the significance which Loeb ascribes to resemblances between plant and animal responses to light.

Amoeba, which as we have seen reacts to a change of light intensity by a checking of movement at the point affected, appears when tested by light passed through differently colored filters to react in the majority of cases most markedly to blue, although there are individual variations: some individuals respond most definitely to violet, others to green or yellow, and still others to red (467). The difference is merely in degree of response, and we can infer nothing about a qualitative differentiation of conscious accompaniments. In *Hydra*, which comes to rest in moderately illuminated regions, blue and green light seem to be a better substitute for white light than are red and yellow (791). Schmid (661) says that red and yellow affect the sea-anemone *Cereactis aurantiaca* differently from blue and green, but does not state wherein the difference consists.

Graber (266) attempted to test the color discriminations of a great many different animal forms by observing their preferences for differently colored lights. As we have already seen, where an animal displays no preference or choice between two stimuli, it by no means follows that the stimuli are not discriminated: they may produce different sensation qualities which are equally agreeable or disagreeable to the animal. When earthworms were the

subject of tests by the Preference Method, it was found that if a choice was offered between two compartments, one illuminated with diffuse daylight, the other dark, and if the number of worms in each compartment was counted at the end of every hour, those in the darkness were on the average 5.2 as many as those in the light. If ground glass was substituted for the dark screen, making the compartment under it about half as light as the other, the number in the lighter compartment was about .6 of the number in the darker, though still moderately light, compartment, showing that the worms were sensitive to comparatively small differences in intensity. When colored glasses were placed over the compartments, the following results were obtained: the worms preferred red to blue even when the former was much lighter than the latter to the human eye; they preferred green to blue under similar conditions, and red to green. They emphatically preferred white light from which the ultra-violet rays had been subtracted to ordinary white light, 6.7 times as many being found in a compartment covered by a screen impervious only to ultra-violet rays. It would thus appear that in determining avoidance, blue light is the most effective; on the other hand, Yung (833) finds the effect of colored rays on the earthworm to be proportional to their intensity, the green and yellow regions of the spectrum being most effective.

It is thus clear that when an animal discriminates between rays of different colors, the discrimination may be based merely on the intensity of the rays, either in themselves or in the effect which they have on the organism, rather than on their wave-length or color. Minkiewicz offers as evidence of true color discrimination in a Nemertean worm, *Lineus ruber*, the fact that he could alter its reactions to

colored light while its response to white light remained unchanged. When placed in diluted sea water, the animal would, after a day, direct itself toward violet rays, although still negative in response to white light. On the fourth day the ordinary "chromotropism" was restored; that is, the worm sought red rays. After two or three weeks of life in the diluted sea water, on being restored to ordinary sea water the worm again showed inverted chromotropism, becoming "positive" to the violet rays, while still "negative" to white light. Moreover, intermediate stages in the passage from the red- to the violet-seeking phase were observed; a stage where, still positive to red, the animal ceased to distinguish red from yellow, and others where it sought violet, but had become indifferent to green and yellow. These stages lasted for several hours, but corresponding ones were not observed during the passage from the violet phase back to the red phase: perhaps they occurred too rapidly to be noted (493).

Hess (314), on the other hand, concludes the total color-blindness of the marine worm *Serpula* from the fact that when tested by the direction in which it turned when subjected to light passing through differently colored glass, it showed evidence that the yellow-green had most effect, and that the effectiveness diminished rapidly towards red, slowly towards violet: in other words, that the brightness effect of the colors was like that shown in the case of a color-blind human being.

Hess (306) also studied the comparative effectiveness of different colored rays on the eyes of cephalopod mollusks by measuring with a special instrument the degree of expansion or contraction of the pupil produced by the various colors. He found that the yellow and green rays produce much more effect than the red and violet rays. Since this

is true also of the color-blind human eye, he argues that the animals tested are totally color-blind. He holds, in fact, that all invertebrate animals are totally color-blind, on the same evidence. The feet of starfish belonging to the *Astropectinidæ* are, he says, very sensitive to light: red light has little effect on them, blue and green light, even when much darker than red to normal human vision, decidedly more effect, as they would have for a totally color-blind human being. The same results appear in the case of the sea-urchin.

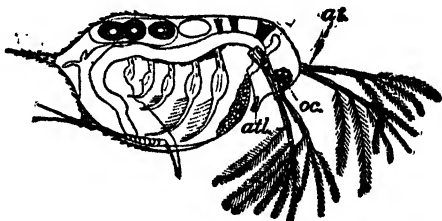


FIG. 10.— *Daphnia*. *at*, antenna; *all*, antennule; *oc*, eye. After Yerkes.

A human being's sensitiveness to light is increased when he remains in darkness for some time. This effect, called darkness adaptation, appears according to Hess in the *Astropectinidæ* (313).

The problem as to whether light of different colors produces different sensations in the crustacean consciousness was the subject of experiments a number of years ago, in which the Preference Method was used. Lubbock (442, 443) arranged to have a sunlight spectrum thrown on a long trough containing *Daphnias*, tiny crustaceans belonging to the lowest subclass, that of the Entomostraca (Fig. 10). *Daphnia* is ordinarily positive in its response to light, that is, it seeks light. At the end of ten minutes glass partitions were slipped across the trough at the approximate dividing lines between the spectral colors. The number of animals in each compartment was then counted. The experiment was repeatedly performed, and the greatest number was always found in the yellow-green region, Bert

obtained similar results with the use of an electric light spectrum; but besides throwing all the colors at once upon the vessel, he allowed each color to act separately through a narrow opening, and noted the speed of the positive response produced. That the "preference" shown for yellow-green light is not a matter of color vision, but of response to the greater intensity of the light in this region of the spectrum, was suggested by Bert (46), and Merejowsky showed that the larvæ of *Balanus* and *Dias longiremis* manifested no color preference when the colors were made of equal intensity (484). Lubbock attempted to prove the existence of qualitative as distinguished from intensive discrimination by various modifications of the experiment, but without entirely conclusive results (444, pp. 221 ff.). Yerkes, working on *Simocephalus*, a form closely related to *Daphnia*, found that when a gaslight spectrum was used, the animals collected in the red-yellow region, that of greatest intensity for such light; and that if this region had its intensity diminished by a screen of India ink or paraffine paper, the crustaceans moved out of it (799). This seemed strong evidence that the apparent color reactions of these animals were really responses to differences in the intensity of the light. Hess (306) studying the movements of the eyes of *Daphnia* when subjected to light of different colors, finds another case of total color-blindness, and Erhard (207) gets similar results on *Simocephalus* when the light is reflected from colored surfaces. Nevertheless, there is evidence that colored rays have an effect on these crustaceans that is not wholly dependent on their intensity; evidence, that is, in favor of color vision. When *Daphnias* have been kept for some time in light of a certain intensity, an increase in the intensity makes them avoid light, while a decrease in intensity makes them seek

light. But if a blue screen is interposed between the light and the animal, in spite of the fact that the intensity is thereby diminished, the *Daphnias* avoid it; if yellow light is added to white light, in spite of the fact that the intensity of the light is thereby increased, the *Daphnias* seek it. These results were obtained by Von Frisch (248), who is as determined to find color vision in invertebrates as Hess is to disprove it. Ewald (213) reports that of the *Daphnias* under his observation one group sought the light, which was in this case most effective in the green-yellow regions, but that another group avoided light, and for these the most effective region was the blue-violet, so the effect of colored rays was independent of intensity. He reports, however, that certain colored rays could be replaced by colorless rays without affecting the responses of the *Daphnias*; these rays were the red and green ones. He therefore concludes that *Daphnia* is not totally color-blind, but red-green blind. This, as we shall see, is Von Frisch's belief with regard to certain other invertebrates. Ewald thinks he has also evidence in the case of *Daphnia* of simultaneous contrast and successive contrast, such as human vision shows. The successive effect (negative after-images) occurs for both color and brightness stimuli, and is shown by the fact that the animals reverse their reaction to the same white light according as they have been exposed previously to white (or blue) light, or to darkness (or yellow light). Simultaneous contrast Ewald concludes from the observation that when the region surrounding a constant stimulus light is brightened, the reaction of the animals tends to become positive, that is, they move towards the light; darkening the surroundings makes them move towards the same light. This effect, it is argued, is due to the stimulation of the side regions of the eye: now, since

colors have no special influence in producing these simultaneous contrast phenomena, Ewald concludes that the side regions of *Daphnia*'s eye, like those of our own eye, are totally color-blind. All of which seems a heavy weight of inference to depend from rather slender evidence.

That *Daphnia* seeks a region affected by the ultra-violet rays of the spectrum in preference to darkness, although the two look alike to our eyes, was shown by Lubbock (444). On the other hand, Loeb (431) and Moore (502) report that the action of ultra-violet rays instantly makes *Daphnia* avoid the light containing them, and it appears that these rays, which are without effect on the human eye, exert their influence through the eye of *Daphnia*, since individuals without eyes are unaffected by them (300).

Adaptation to darkness apparently takes place in the eye of *Daphnia*, for individuals which have been a long time in darkness will respond to a lower intensity of light than those which have been long exposed to illumination (174). Experiments on the effect of intermittent and continuous lights of equal intensity on the movements of the *Daphnia* eye indicate that the Talbot-Plateau Law, according to which such lights are identical in effect, holds for the vision of this crustacean as for the human eye (212). It is this law which enables us to measure the grey produced by a rapidly revolving disk of black and white sectors as equal in brightness to the amount of light reflected by the sectors at rest.

Experiments on the reactions of the crayfish, which has a moderately strong tendency to avoid light, show that when light falls vertically through red glass the animal seeks it in preference to darkness: no marked preference is indicated when the light is passed horizontally through red glass (40). No clear evidence of color discrimination ap-

pears here. Hess (306), of course, holds that all crustaceans are totally color-blind, arguing from his results on the relative stimulating effect upon them of different spectral colors. Minkiewicz (494, 495), on the other hand, believes he has evidence of color discrimination in certain crabs. The hermit crabs, for instance, are naturally attracted to light, but when subjected to colored lights they do not seek them in the order of their intensity. Green is the most attractive color, violet next; then the order is "blue, yellow, red, and black." He finds it possible with crabs, as with worms (see page 147), to reverse the response to white light without reversing the response to color (493). Minkiewicz's most remarkable observations were made on certain crabs (*Maia*) which have the instinct possessed by many crab species of attaching to their shells foreign objects, bits of seaweed and the like, serving the purpose of making them less conspicuous in their ordinary environment. When these crabs are kept for some time in an aquarium lined with a certain color, their subsequent behavior is modified in two ways. (1) On being given bits of paper some of which are colored like the aquarium, while others are of a different color, the crabs select for decorative purposes the bits that match their surroundings. (2) When placed in another aquarium offering a choice between two compartments, one with walls matching those of the tank they have left, the other with differently colored walls, the crabs choose the former. Two American investigators have performed experiments similar to these. Pearse (567) fails to get any evidence that when crayfishes, spider crabs, crab spiders and caddis fly larvæ are kept in colored boxes they develop any tendency to choose later an environment of the same color. On the other hand, Stevens (693), working with a Pacific coast crab which has

the decorating instinct, finds that it does acquire such a tendency, but that it does *not* learn to decorate itself with colors matching its surroundings. The acquired "chromotropism," or tendency to seek a certain color, in crabs might be interpreted as merely a response to the brightness of the colors, not to their color as such; that is the crabs may after all be totally color-blind, seeing the colors as grays. Stevens found indications that green comes nearest to white light in its effect on the animals, by noting the promptness and accuracy with which they faced the light.

Experiments have been made on color discrimination in spiders: some by the Preference Method, where the spiders showed an inclination for red when offered a choice of compartments illuminated through red, green, blue, and yellow glass (570); others by attempting to form an association between paper of a certain color and the spider's nest. This latter, containing eggs, was surrounded with colored paper, and when a spider had become accustomed to going in and out over the paper, another color was substituted, and a false nest made in another place, surrounded by the original strips of paper. The spider under these circumstances showed some confusion and tendency to go to the false nest. It is obvious that this method takes no account of the possibility that the spider was reacting only to the intensity of the colored rays and not to their color as such (571).

On the color sense of insects there are, first, the old experiments of Graber by the Preference Method, whose most definite result was to show that positively phototropic, that is, light-seeking, insects prefer colors containing the ultra-violet rays, while the negatively phototropic or light-avoiding ones prefer red, from which these rays are absent. No proof that the discriminations were made on the basis

of color proper rather than brightness was forthcoming (267). Similar observations were made by Lubbock on ants, which in their underground life are negatively phototropic, the eggs and larvæ apparently needing darkness in order to develop, but on their foraging expeditions are comparatively indifferent to light. They showed a preference for red when tested, and a tendency to avoid the ultra-violet rays, so marked that they preferred bright daylight from which these rays had been extracted by chemical screens, to darkness that contained the ultra-violet rays (441, pp. 207 ff.). Graber suggested that the ultra-violet rays produce a skin sensation in the ants; but Forel agrees with Lubbock that the effect is visual, because he found that varnishing the eyes made the ants indifferent to ultra-violet (231). Ants of the family *Lasius* seem to be normally insensitive to these rays (235). It is just possible, then, that a visual sensation of quality wholly foreign to our experience may accompany the action of ultra-violet rays on insects. Loeb has noted that the relative effect of violet and ultra-violet vibrations, as compared with that of the rest of the spectrum, is greater, the less developed the visual organ (419). Termites, which seek darkness, prefer red to blue colored glass (6).

Lubbock's experiments on the color sense of bees are more to the point than those on ants, for they were made not by the Preference Method, but by associating a color with food. No precaution, however, was taken against the brightness error. He found that bees which had eaten honey from blue paper would pick out the blue pieces from a number of differently colored papers, whose positions were altered during the experiments (441). Forel got similar results, and reports that a bumblebee thus trained selected all the blue objects in the room for special ex-

amination (231). Lubbock's tests with wasps gave negative results. Lovell (439) and Turner (725) also infer color vision in the honey-bee from its ability to pick out objects of the same color as that on which it has recently found food: the former takes no account of the brightness error, while the latter holds that it has been sufficiently eliminated by the fact that the color identifications were made by the bees under varying lights and shades out of doors. This, however, is probably an inadequate precaution. Von Frisch (246) offers more convincing evidence of color vision in the bee, and thinks he has indications that bees are red-green color-blind. His experiments were performed in the open air. Having trained the bees to come to strips of yellow paper, on which food was placed, he mingled such strips, without food, among strips of thirty different shades of gray. The bees, he reports, were able to make the discrimination, and to do equally well when blue was used: they failed, however, with red, confusing red-violet with blue, and dark red with dark gray. In another article (247) he says that a certain bluish green also was confused with gray. This general method, where a large range of grays is used and an animal proves capable of discriminating a color from any or all of them, is the best way of eliminating the brightness error. The use of colored papers in experiments on color vision in animals is open to criticism unless some precaution is taken against the possibility that something in the surface texture or grain of the papers may help the animal to distinguish. This possibility Von Frisch guarded against by varnishing the papers, a proceeding which did not affect the behavior of the bees.

Hess (312, 315), anxious to defend his theory of the total color-blindness of all invertebrates, repeated Von Frisch's

experiments and could not confirm his results. Using colored lights of measured intensities and studying their effect in causing the bees to collect under them, he compared these effects with the influence of the various colors on the reflex contraction of the pupil in human beings. He found that the smallest differences in intensity to which the bees reacted were those just perceptible to the human eye, and that the relative effect of different colors was like their relative effect on a color-blind human being. He reports similar results with butterflies. Hess thinks this method, which deals with reflexes, superior to any method which, like Von Frisch's, involves learning on the part of the animals. But again we may remind ourselves that it does not follow that because a human being who finds the yellow-green, rather than the yellow, the brightest spectral region, is totally color-blind, therefore an animal, especially an invertebrate animal, the chemical substances in whose eye may have no resemblance to those in the human eye, is color-blind if it shows these reactions to the different regions of the spectrum. Hess's method is defective just because it deals with reflexes whose stimuli are intensity differences. If an animal is capable of distinguishing both intensity differences and color differences, the use of reflexes that depend on the former is a poor way of studying the capacity to discriminate the latter.

We have already noted the dispute as to how far visual sensations in general are involved in the reactions of bees to flowers, and have seen that Plateau maintains their relative unimportance in this connection, as compared to smell. Besides the experiments which we have quoted on pp. 104 f., he adduces the facts that he could never persuade insects to alight upon artificial flowers, though these were not distinguishable by human eyes from real ones (600-

602); that bees show no preference for flowers of any particular color (603); and that they often make errors, in alighting on closed buds, seed pods, and wilted flowers, which indicate defective vision (605). But Josephine Wéry and others have noted that bees do seek artificial flowers (778). Even Plateau does not deny that an insect may perceive flowers from a distance, "whether because it sees the color in the same way that we do, or because it perceives some kind of contrast between the flowers and their surroundings" (603).

Von Buttel-Reepen (114) gives one or two instances to show that the color perception of bees is sometimes influential in helping them to recognize their own hives. He reports a case where a stock of bees had been driven from their hive and scattered. The front of the hive was blue. Some of the bees tried to find their way into other hives, and selected for their efforts those which had blue doors.

It will be remembered that Loeb is convinced that the relative effect of the different regions of the spectrum on invertebrate animals is identical with the effect on plants; that is, strongest for the violet end of the spectrum. This position has no significance for the problem of color discrimination, but obviously Loeb and Hess are sharply opposed as to the facts. Recently Gross (271) has used colored spectral lights of carefully equated intensity, and a method which permits measurement of the exact amount of light effect, in deflecting an animal from its course of movement. Adult blowflies, fruit flies, and moths, as well as larvæ, were used as subjects. All the lights were made of equal intensity, whereas in the ordinary daylight spectrum the yellow region is most intense and differences of intensity exist all along the line. Under these conditions, Loeb's contention was confirmed

and Hess's overthrown for all the subjects except the larvæ of the blowfly; that is, the insects were more strongly affected by blue than by yellow or green. But the blowfly larva was more strongly affected by green than by any other colored light. It responded, in other words, as Hess and his pupil Weve (779) had found it to do.

§ 41. *The Problem of Visual Qualities: Amphioxus and Fish*

The vertebrate eye differs in origin and structure from any form of invertebrate eye, the most striking difference in structure being the location of the pigmented layer of the retina behind the nerve fibre layer, a location which is responsible for the existence of the blind spot in the vertebrate eye, where the trunk of the optic nerve breaks through the retinal layers. Another point of unlikeness consists in the fact that the invertebrate optic nerves do not cross on their way to the brain, while in the vertebrates there is either total or partial crossing of the fibres.

The reactions of *Amphioxus* to light offer as chief evidence that they are accompanied by a specific sensation quality the fact that they may be fatigued independently of other reactions. The only structures suggesting a visual function are pigment spots on the back near the head, and other pigment spots distributed down the back. *Amphioxus* makes negative responses to light, especially when the light, from which heat rays have been extracted by passing it through water, is directed at any point on the back, the most sensitive region lying just behind the eye-spot (406, 543). Fatiguing the light reactions had no effect on response to other forms of stimulation (543). Attempts to test the color "preferences" of *Amphioxus* by illuminating

different parts of a trough with differently colored lights gave negative results (406). Hess (306) found that the maximal effect on the activity of *Amphioxus* was exerted by the yellow and green rays, the red and violet being much less effective; hence he concluded that as in all invertebrates, so in this rudimentary vertebrate, total color-blindness exists.

True skin sensitiveness to light has been observed in larval lampreys, which will give negative reactions even when the optic nerves are cut (540), and in cave-dwelling blind fish (201). Parker, however, finds no other fish in which it exists, although it is quite common in amphibians. He therefore reaches the conclusion that in vertebrates, skin sensitiveness is not a primitive form of visual sensibility, from which vision by the eye has been derived, but a "secondarily acquired peculiarity." He points out that the fish and amphibians which show it are freshwater animals, whereas the primitive vertebrates were certainly marine (545).

Among the many animals whose supposed color preferences Graber tested were two species of fish, but no convincing proof of their powers of color discrimination was obtained (267). Bateson (25) placed food on differently colored tiles, and observed that the fish picked it off most readily from white and pale blue, and least readily off dark red and dark blue; which establishes little save that the bait was probably more conspicuous on the white and pale blue. Professor Bentley and the writer (757) got good evidence that the common brook chub could distinguish between red and green paints, by training it to bite at forceps to which red sticks were attached, and to refrain from biting at similar forceps carrying green sticks. The possibility of guidance by smell or by the position of the for-

ceps was ruled out, and the fish could identify the red forceps whether they were to the human eye darker or lighter than the green. It is not, however, a sufficient guard against the brightness error to use human judgments of brightness as a standard. Reighard (631), similarly, trained the gray snapper to avoid minnows dyed in certain colors and select those dyed in other colors, several brightnesses differing to the human eye being used, but the brightness error not being more fully eliminated. Bauer (27) believes he has secured evidence that fish discriminate colors, and that certain fish are afraid of red, but the general character of his methods and conclusions does not inspire confidence. Hess (304, 308) is convinced that the spectrum is seen by fishes with the same distribution of brightnesses that is characteristic of the color-blind human eye, and makes the inference, which we have previously challenged, that total color-blindness must exist in such a case. Von Frisch (245), on the other hand, argues that fish possess color vision. He has shown their ability to pick out a color from a whole series of grays. He points to the fact that in the spawning season many fish assume bright colors and patterns; these, he urges, must have some influence in bringing the sexes together (243). Hess (310) in opposition to this points out that such colors would not be visible below a certain depth of water; Von Frisch replies that most of the fish which show them spawn in shallower waters. One can hardly, however, infer color vision from the existence of such colors, for they may be only incidental effects of the physiological state of the animals, and without any influence on their behavior. A more persuasive line of argument is derived from the way in which various flatfish change their markings and colors to suit the ground on which they lie. Von Frisch (240)

studied this phenomenon in the case of the fish *Phoxinus laevis*. If two fish whose skins are, at the time, of equal brightness, are placed one on a yellow ground, the other on a gray ground, and these grounds are properly chosen as to brightness, the fish will not alter their own brightnesses, although if either ground is made lighter or darker a corresponding change occurs in the skin of the fish lying on the altered ground. When the fish remain at the same brightness, then, it may be inferred that the "brightness values" of the two grounds are identical. But after a few hours, it will be found that the fish on a yellow ground shows a yellow stripe which does not appear on the other fish (see also 277). Mast (475) has made a very thorough study of this phenomenon in the case of the flounders *Paralichthys* and *Ancylopsetta*. These fishes become strikingly bluish on blue grounds, greenish on green grounds, and so forth, adapting themselves to blue, green, yellow, orange, pink, and brown, and less successfully to red. The color changes are brought about by certain pigment-controlling mechanisms in the skin, which are connected with the sympathetic nervous system. But the color stimulus acts through its effect on the eyes: the changes do not occur if the eyes are covered. Moreover, the effect of the stimulus received by one eye is modified by that of the stimulus received from the other eye: if one eye is on a black ground and the other on a white ground, the skin becomes gray. Mast succeeded in showing that the rate at which alternating black and white sectors must follow each other in order to fuse into a continuous gray is the same for the eye of the flounder as for that of the human being: he placed the fish over a rotating black and white disk and noted the speed of rotation required for the fish to become gray instead of mottled black and white.

Watson (771) does not think these observations sufficiently prove color discrimination on the part of the fish. He says, "Ordinarily we mean when we say that an animal is sensitive to difference in wave-length that such stimuli play a rôle in the adjustment of the animal to food, sexual objects, shelter, escape from enemies, etc. *i.e.*, that such stimuli initiate activity in arcs which end in the striped muscles." Because the changes of color are produced not by such arcs, but by the sympathetic nervous system, Watson thinks color vision not proved; "we can easily conceive," he says, "of mimicry of this kind taking place in an animal whose retina does not contain the physico-chemical substances . . . necessary to initiate response to differences in wave-length." Since the changes of color are induced by differences in wave-length and induced through the retina, we may reply that it does not seem easy, or in fact at all possible, to conceive the absence of such photo-chemical substances from the fish's retina. Moreover, Mast finds that fish which have thus become adapted to a given color will seek that color: this is an activity involving the striped muscles.

On the whole, the weight of evidence is at present in favor of the possession of color vision by fish.

§ 42. *The Problem of Visual Qualities: Reptiles and Amphibia*

Skin sensitiveness to light has been demonstrated in certain amphibians. The response of the frog to light persists when the animal is blinded, although in the normal animal the eyes are involved in the reaction, since it occurs when the skin is covered and the eyes left intact (405, 538). The skin of salamanders also is sensitive to

light (196). The nature of the "dermal light sensation" remains a mystery. It can hardly, in frogs, be a painful irritation, since it produces a positive response; and it is not due to heat rays, for it occurs when these are intercepted by passing the light through water. As Parker says, radiant heat and light, "distinct as they seem to our senses, are members of one physical series in that they are both ether vibrations, varying only in wave length" (538). While, then, the nerve endings in human skin are sensitive only to the slower of these vibrations, the heat rays, those in the skin of the frog may respond to the whole series, with what accompanying sensation qualities we cannot say. It is interesting to note that Pearse (566), working with frogs and salamanders, normal and blinded, finds that red light, which stands nearest to heat in vibration frequency, is most effective for the blinded animals, blue light for the normal ones. In the young of frogs and salamanders it has been shown that the skin nerves are the source of dermal reactions to light.

The frog's eye is sensitive to light rays from all the spectral regions visible to man; the distribution of brightnesses in the spectrum is like that of normal human vision, and the dark-adapted eye shows a shift of the brightness values to correspond with those of the dark-adapted human eye. One method by which these results were obtained was that of testing the electric effect (action currents) of stimulating frogs' eyes with light of different colors: the maximum effect for the light-adapted eye was in the yellow green, that for the dark-adapted eye was in the yellow (324 a). Another method was to illuminate food with light of different colors and to observe in what lights it was most readily seized. From the results Hess (305) concludes that amphibian vision is qualitatively like that

of man. Babák (11) has studied the effect of different colors on the frog's breathing; its rate and the movements involved in "throat" and "lung" breathing. The fore-brains of the animals had been removed, a proceeding which makes the breathing of the resting animal more regular. He found that each color produced a breathing curve of a certain specific pattern, and concluded that the colors have specific effects on the eye independent of their intensity.

The results with turtles, which are reptiles, correspond to those for amphibians, except that Hess (305) finds the spectrum shortened at the violet end; that is, the turtle does not see beyond the blue. The method used was that of illuminating food with differently colored lights. Hess explains this shortening of the spectrum by the fact that in the turtle eyes, as in those of all birds, a few fishes, and Ornithorhyncus, there are attached to the ends of the cones transparent colored globules like little drops of oil. They are in the turtle mostly red and orange, and would act, Hess thinks, like spectacles of colored glass to cut off the blue and violet rays. The fact that adaptation to darkness apparently occurs in the turtle is of interest because its retina is lacking in rods. The rods, then, cannot be, as they have sometimes been supposed, essential to the process of darkness adaptation.

§ 43. *The Problem of Visual Qualities: Birds*

Many experiments have been made on color discrimination in birds. Most of the older ones were conducted by the method of training the birds to choose between differently colored papers (611), or between compartments illuminated through differently colored glass (647). These

experiments made practically no attempt to guard against the possibility that the birds were reacting to differences in the brightness of the lights. Another method used by Katz and Revesz (395) was that of scattering grain on grounds of different colors and noting how often the grain was picked from the several grounds. The positive result of this research was that while fowls with light-adapted eyes pecked equally often at grains on yellow, green, red, and violet grounds, those with dark-adapted eyes never pecked at grain on the red ground. This indicates a process of darkness adaptation like that in the human eye, which sees red as very dark in faint light. In a later investigation the same workers tried scattering red, blue, and green grains of various saturations, mixed with grains stained four different shades of gray. All the grains were stuck fast to the ground except those of a particular color. The fowls showed an ability to discriminate which was about equal to that of the normal human being. It cannot be said, however, that these experiments satisfactorily eliminated the brightness error, since so few shades of gray were used.

The effect of different colored rays on the pupillar reflex of birds was studied by Hess (303). For day birds, he found that the maximal effect was produced by the yellow rays; for owls, by the yellow-green. That is, the day birds showed the brightness distribution characteristic of the light-adapted human eye with color vision; the night birds the distribution of total color blindness, or darkness adaptation. By his method of observing under what illumination the animals could find food, Hess obtained results leading him to conclude that day birds have a spectrum shortened in the violet end, a fact which he ascribes to the effect of the oil globules in the retina; and that the spectrum for

owls is somewhat longer. Watson (773), on the other hand, working with a more exact apparatus, concludes that the spectrum is visible to the chick and the homing pigeon within the same limits as to man. A study of the electric currents generated by the action of light on the eyes of day and night birds gives evidence confirming the hypothesis that the latter are color-blind: in the day birds, each color gives a characteristic deflection of the galvanometer, not due to its intensity, while no such differences appear for the eyes of night birds (403). Breed (101, 102), using colored screens through which the light was passed, and offering a choice of passages differently illuminated, obtained evidence of color discrimination in the chick. The preference of the chicks for one color rather than another appeared to depend on the relative brightness of the colors, since it could be reversed when their brightnesses were sufficiently altered. When a blue and red were found between which the chick showed no preference, this was taken as an indication that they looked equally bright to the chick. The bird could, however, be trained to choose one of these two colors; hence the conclusion was reached that it could probably react to a difference in color and not merely to one in brightness. The evidence for color vision in birds has lately been made practically conclusive by the careful experiments of Lashley (413) on the domestic fowl. He used spectral light whose intensity was accurately controlled. The ability of the fowl to distinguish red and green was demonstrated under the following conditions, which ruled out the possibility of discriminating by brightness differences. (1) Each of the lights was alternately reduced to threshold intensity, while the other remained at full intensity. (2) White light of a constant intensity was substituted for each colored light in turn.

(3) Each light was in turn exposed alone, one passage being left dark.

Indications of the presence of darkness adaptation in the chick appeared from the facts that light adapted chicks chose red and yellow rather than green, while for dark adapted chicks the preference was reversed.

Rouse observed that differently colored lights had on the average different effects in quickening the rate of breathing in the pigeon; the strongest effect being produced by blue, the weakest by red (648).

§ 44. *The Problem of Visual Qualities: Mammals*

The earlier experiments on the visual discriminations of mammals, like those with other animals, failed to reckon adequately with the brightness error, the possibility that discriminations between colors are made as a color-blind human being would make them, the colors being seen as different shades of gray (138, 140). The first method, as we have seen, which suggested itself as a means of eliminating this error was that of showing that an animal could, or could not, distinguish a color from the gray which a light-adapted human being would see in its place. Such a gray can be determined by the so-called "flicker method." If a disk be made of a colored and a gray paper, when it is rotated a little too slowly to give a smooth mixture, the peculiar appearance of "flickering" will be observed if the color and the gray are not of equal brightness, but will disappear when a gray equally bright with the color is selected. The determination of this equivalent, however, has really no bearing on the problem of color vision in animals. If they are color-blind, their difficulty would more probably lie in distinguishing

between a color and its brightness equivalent for the color-blind or dark-adapted human eye; and quite possibly the brightness which they see instead of color may be unlike the brightness value of that color to either the light-adapted or the dark-adapted human eye.

Kinnaman's (401) color tests on monkeys, from which he concluded that they possess color vision, employed only the older methods of getting rid of the brightness error: the monkeys, which had learned to identify a vessel covered with a particular colored paper as containing food, were shown to be unequal to the discrimination between gray papers whose brightnesses were to the human eye the same as those of the colors. It was also shown that a colored glass could be picked out many times from among three others covered with gray paper of the same brightness as the color, to human vision. In Cole's (134) demonstration that raccoons can distinguish colors, the colors used were equated in brightness for the human eye by the flicker method.

The experiments of Yerkes on the dancing mouse (820) brought into clear relief the danger of trying to eliminate the brightness error by the use of grays equal in brightness with the colors to the human eye. His method consisted in teaching the animals to associate one of two differently illuminated compartments with an electric shock. The intensity of the illuminations could be regulated by varying the distance of the lights from them. When only white lights were used, Weber's Law was found to hold for the one mouse tested: the animal could distinguish a difference in the brightness of the compartments amounting to about one-tenth of their absolute brightness, within certain limits of absolute brightnesses. Light blue and orange, green and red, violet and red, were discriminated

even when their brightnesses were considerably varied. Yet the probability appeared that these discriminations were based merely on brightness differences, for after a mouse had learned to choose green rather than red, when it was offered a choice between light and darkness, it uniformly preferred the former, although untrained mice showed no such preference. Apparently, then, the green had been previously discriminated simply as the lighter of the two impressions, and to the eye of the mouse, as to that of the color-blind human being, red looks an extremely dark gray.

In some experiments of the writer's (756) on the rabbit, the method was used of presenting a color with various grays, in successive experimental series, and finding whether or not there existed a gray with which the color was confused. This is the only adequate way of dealing with the brightness error. We found that while the rabbit could be taught, by rewarding it with food for right choices, to distinguish a standard red paper from a number of different gray papers, it invariably failed when a very dark gray, almost black, was presented with the red. Two objections which have been urged against the use of colored papers were met in these experiments. In the first place, it is argued that papers of different colors may differ in surface texture: the possibility that our rabbits reacted to this clew we eliminated by occasionally substituting red and gray velvets for our red and gray papers, a change that did not at all affect the rabbits. Secondly, it has been urged that when colored papers are pasted on cards, they are apt to show wrinkles that might identify them: this we obviated by pinning on our papers afresh in successive experiments.

Obviously, however, since colored papers do not give

pure colors; since, that is, they reflect to the eye light of wave-lengths besides that of their predominant color, the use of pure spectral light is to be preferred. The apparatus by which such light can be used with its intensity accurately controlled is very elaborate, and was devised by Yerkes and Watson (831). Using this apparatus, the Watsons (772) found that rats and rabbits failed to distinguish between red and darkness. A similar indication had been previously obtained by Waugh (775) on the gray mouse; he found that red filters and pigments could be distinguished from gray when the two were equal in brightness to the human eye, but that the discrimination tended to disappear when the red was made lighter, and to improve when it was made darker.

The dog and cat also suffer under the imputation of color-blindness. Tests by Pawlow's method on the dog failed to indicate that it can react to color differences as such (830). Smith (687), it is true, working with colored papers, argues in favor of the dog's color vision from the fact that the dogs showed some evidence of learning to distinguish the colors from all the grays used. De Voss and Ganson (184) found that none of the six colored papers they used could be discriminated by cats from all the shades of gray in their series: each color was confused with some particular gray. Even the monkey is suspected of color-blindness: Watson (768) reports as the chief result of his experiments with this animal that red has little or no stimulating power upon it.

CHAPTER VIII

SPATIALLY DETERMINED REACTIONS AND SPACE PERCEPTION

§ 45. *Classes of spatially determined reactions*

MODIFICATION of the behavior of animals with reference to the spatial characteristics of the forces acting upon them appears at the very beginning of the scale of animal life, and throughout is quite as important as modification with reference to the kind or quality of such forces. It assumes a number of distinct forms. Some of these suggest to us, interpreting them as we must on the basis of our own experience, no conscious aspect at all; they seem rather mechanical effects upon a passive organism. In other cases, it appears possible that the mental process which we know as space perception, involving the simultaneous awareness of a number of sensations consciously referred to different points in space, may accompany the reaction of an animal with reference to the spatial relations of its environment. And sometimes we can only say that differences in the space characteristics of a stimulus may modify the accompanying sensation in some manner which yet apparently does not involve space perception as we know it.

Our task in the following pages will then be to examine the different ways in which animal behavior is adapted to the spatial characteristics of stimuli, and to ask which of these suggest as their conscious accompaniment some form of space perception. A classification of spatially

determined responses that is not, indeed, ideally satisfactory, but may serve our purpose, divides them into five groups:—

1. Reactions adapted to the position of a single stimulus acting at a definite point on the body.

2. Reactions to a continuous stimulus, which involve the assumption of a certain position of the whole body with reference to the stimulus: orienting reactions.

3. Reactions to a stimulus that moves, *i.e.*, that affects several neighboring points on the body successively.

4. Reactions adapted to the relative position of several stimuli acting simultaneously.

5. Reactions adapted to the distance of an object from the body.

These forms of behavior will be successively discussed.

§ 46. *Class I: Reactions to a Single Localized Stimulus*

Responses to stimulation that are adapted to the point of application of the stimulus are to be found among very simple animals. They may be subdivided into three groups: first, cases where the part of the animal that reacts is the part directly affected by the stimulus; second, cases where the whole animal reacts by a movement in the appropriate direction; and third, cases where a part of the body not directly affected by the stimulus moves toward the point stimulated.

1. *Amoeba* furnishes an example of the first class. Its negative reaction occurs by the checking of protoplasmic flow at the point where a strong mechanical stimulus affects the body; its positive reaction by a flowing forward of the protoplasm at the point where a weak stimulus acts, and its food-taking reaction by an enveloping flow on both sides of

the point stimulated. This would seem to be the most primitive way of adapting response to the location of a stimulus: the effect is produced just where the force acts, as it might be upon a piece of inanimate matter. In no animal with a nervous system, probably, is the process quite so simple. The bell of the jellyfish contracts at the point where a stimulus, mechanical or photic, is applied; yet although these responses are made when the nervous system is thrown out of function, they occur more slowly, and in the normal animal the nervous tissue is probably involved, while, of course, a long conduction pathway is traversed when, to use a familiar illustration, the baby pulls back its hand from the candle flame.

2. *Paramecium* and other infusoria, planarians, the earthworm, and various other animals give us illustrations of movements of the entire body differing according to the point affected by a single stimulus. If the front half of *Paramecium* be touched, the animal gives the typical avoiding reaction of darting backward and turning to one side; if the hinder end be touched, it moves forward (378, p. 59). On the other hand, it makes no difference in its reactions to stimuli affecting either side of the body; the turning is always to the aboral side even when the stimulus comes from that direction (378, p. 52). If strong mechanical stimulation be applied to the head end of a planarian, there is a response which seems to belong under type (1): the head is turned away from the stimulus. If the hinder region is touched, strong forward crawling movements of the body are produced. The positive reaction in the planarian, turning the head toward the stimulus, also suggests type (1), but in reality it has been shown by Pearl to be a far more complex affair than the mere flow of protoplasm at the stimulated point, and to involve the contraction of several

sets of muscles (561). The earthworm creeps backward if the front half of the body is affected, turns away from a stimulus applied to the side of the anterior end, and creeps forward if the stimulus affects the posterior half of the body (377). In general, a reaction of type (2) rather than type (1) will occur in proportion to the degree in which an organism's movements are coördinated and it tends to act as a whole.

3. One of the prettiest examples of the most highly co-ordinated form of response to a single localized stimulus; namely, movement of some other part of the body toward the point affected, is to be found in the swinging over of the jellyfish's manubrium toward the spot on the bell touched by food. "In the typical feeding reaction," says Yerkes, "the manubrium bends toward the food. If during such a movement the piece of food be moved to the opposite side of the bell, the manubrium, too, in a few seconds will bend in the opposite direction, that is, again toward the food" (802). The sea urchin responds to mechanical stimulation by moving the spines toward the place stimulated (735). In the higher animals this form of reaction has largely superseded other methods of adapting behavior to a stimulus acting at a definite point. Where grasping appendages exist, the obvious device is to move them toward the point of stimulation in order either to seize or to remove the object. This involves not merely that the effects of the stimulus shall diffuse so as to involve general locomotor movements, but that the effect shall be exerted very definitely upon a particular set of muscles in a particular way. The "scratch-reflex" of mammals, and the reaction whereby a frog rubs its hind leg on the spot of skin affected by a drop of acid, are further examples.

What can we say regarding the conscious accompani-

ment of the reactions described under these three heads? When a stimulus applied at point *a* brings about a reaction different from that produced by precisely the same stimulus acting on point *b*, are the accompanying sensations different, supposing the animal concerned to be conscious? If they are, the difference must be what has been called a difference in *local sign*. There is certainly no evidence that *space perception* is concerned. Space perception in our own experience always involves the simultaneous awareness of several stimuli. But where a single stimulus only is operative, the fact that reaction to it is modified by its location cannot mean that the relations of that location to the location of other stimuli are perceived. The truth is that space perception is so constant a factor in our own experience that we cannot imagine how a single sensation can be modified in connection with change of place of the stimulus, where space perception does not exist. A touch at any point on the skin of a human being is referred to a definite point in a constricted space, tactile and visual; it is given its proper place in a complex of sensations. What modification of it would correspond to its location if it stood alone in consciousness, we cannot now conceive.

§ 47. *Class II: Orienting Reactions; Possible Modes of Producing Them*

Various forces, such as gravity, light, electricity, centrifugal force, currents of water and air, are all influences causing certain organisms to bring their bodies into a definite position. Such reactions, involving the direction of the whole body with reference to a continuous force acting upon it, are known as reactions of orientation. There are various ways in which they might conceivably take place.

(a) They might be due to the "pull" of a force upon the passive body of an animal. In the case of gravity or of a current of wind or water, if one part of the body were heavier or offered more surface to the force, the position assumed could be explained without supposing any activity on the animal's part. In such a case there would be no reason for thinking of the reaction as conscious.

(b) The response might be due to the effect of a force acting unevenly upon the two sides of the body, and thereby unevenly affecting the motor apparatus on the two sides, thus causing the animal to turn until the forces acting upon symmetrical points were balanced. This, although involving activity on the animal's part, would not, if the force acted directly on the muscles, suggest any conscious accompaniment. If it acted through symmetrically placed sense organs, awareness of the direction from which the force operated might be present.

(c) The orientation might take place by a negative reaction on the animal's part to a definite stimulus given when the animal was in any other than the final, oriented position. If gravity were the force in question, the stimulus might be the pressure exerted within the body by particles of different density or by the fluid or mineral bodies in a statocyst organ. If the stimulus were light, the organism might be oriented by giving the negative reaction when its head entered a region either brighter or darker than the optimum illumination. In such cases, where the ordinary negative reaction is the only one involved, there is no reason to suppose the occurrence of any conscious accompaniment, other than the possible unpleasantness connected with that reaction.

(d) Orientation to gravity might occur through a special-

ized "righting" reaction, given in response either to a stimulus within, say, a statolith organ, or, as in the planarian, to the absence of accustomed contact stimulation on one surface of the body. The reaction in these cases being a specialized one, it is possible that a peculiar sensation quality might be involved.

(e) Orientation might take place through a movement occurring when the position of several stimuli perceived simultaneously was disturbed, and tending to restore them to their original position. This is the principle involved, as we shall see, in explaining the rheotropism or current orientation of fishes, and the anemotropism, or orientation to air currents, of insects, as due to an instinct to keep the visual surroundings the same. And this form of orientation alone suggests a true space perception as its conscious accompaniment.

Such being the conceivable ways in which orientation may be brought about, what are the observed facts? They may be considered under the heads of orientation to gravity, to light, and to other forces.

§ 48. *Orientation to Gravity: Protozoa*

To this form of reaction the term "geotropism" or "geotaxis" has been applied. In various Protozoa negative geotropism, or a tendency to rise against the pull of gravity, has been observed: first by Schwartz in two single-celled organisms frequently classified as plants, *Euglena* and *Chlamydomonas* (667); and eight years later by Aderhold, who suggested, without accepting it, the theory that the orientation may be due simply to the greater weight of one end of the organism's body (2). This view was maintained by Verworn: the action of gravity, he urged, must

be purely passive. It cannot operate as a stimulus to active response on the animal's part, for a stimulus is always a change in environment, and gravity is a constant force (742). This ignores the fact that the animal's relations to gravity may change though gravity does not, and also the fact that the continuous action of light is a stimulus. According to Verworn's theory, the geotropic orientation of a single-celled organism takes place through a series of "little falls" whereby the heavier end is directed downward. Massart opposed this view on the basis of observations which showed that the actual movements of the organisms did not correspond to it, but were the result of active orientation. If response to gravity is passive, then dead animals should fall through the water in the same position as that assumed by living animals when oriented to gravity. Massart experimented with various Protozoa by killing them and studying their positions in sinking, which he found not always the same as the attitudes assumed in response to gravity (461). There is always the possibility, however, that the methods employed to kill may change the specific gravity of some part of the body. Jensen offered the theory that reaction to gravity may be due to the difference in the water pressure on the two ends of the animal. He asserted that when the air pressure on the water was reduced by exhausting the air above, there was an increase in the geotropism, indicating a relative rather than an absolute sensibility to pressure (382), but Lyon points out that this process may affect the animals in various other ways besides altering the air pressure. Increasing the air pressure, or protecting the surface with oil, has no effect upon geotropism, Lyon finds, and he urges that Jensen's theory requires enormous sensibility to pressure differences on the organism's part, as great as that needed by a human

being to note the difference between the air pressure on the head and that on the feet (449). Another suggestion was offered by Davenport (175), namely, that negatively geotropic organisms swim in the direction where the greatest resistance to their progress is offered. This is like one theory put forward to explain rheotropism, or the tendency of animals to swim against currents, and anemotropism, or the "head against wind" movement of insects; and as Rádl (622) first and Lyon (448) afterward pointed out, it assumes the fact to be explained, for only if an animal actively opposes a force, will that force exert more pressure at one point of its body than at another. The theory cannot explain why an animal at rest should be oriented. Another argument that tells against it is offered by experiments showing that animals placed in solutions of the same density as their own bodies, in which, therefore, they have no weight, still display negative geotropism, and that the direction of the response is not reversed when the fluid is made heavier than the animals (449). Lyon's own theory, accepted by Jennings, is that the stimulus for geotropism is furnished by the action of gravity within the body of the organism, upon substances of different weight which exert varying pressures and take up different positions according to the position of the body (449).

Harper (289) in 1911 revived the mechanical theory of the geotropism of *Paramecium*. He argued that an animal which, like this protozoön, moved in a spiral could hardly use the changes of position of internal particles as effective stimuli. The reaction of *Paramecium* can be altered by altering the specific gravity of its body, as by causing it to absorb particles of iron or paraffin. When it has ingested iron, its responses are modified by the neighborhood of a

magnet (290). Wager (751) maintains that geotropism in *Euglena* also is purely passive, due to the fact that the hinder end of the animal is the heavier. Kanda (389) has recently championed the "statocyst" theory of Lyon, as against the mechanical theory, using Lyon's argument that when *Paramecia* are rapidly rotated in an apparatus called a "centrifuge," their front ends are directed outward by centrifugal force and therefore must be heavier, instead of lighter, as the mechanical theory would require. Harper had previously attempted to meet this objection by regarding such a position on the part of the centrifuged animals as due not to centrifugal force but to compensatory movements made actively by the animal. Both the mechanical theory and the "statocyst" theory, then, seem to be still on the field.

It has been shown that the reactions of *Paramecium* to gravity are modified by a variety of conditions. Negative geotropism, in a sense its normal condition, is favored by plentiful food supply and by an increase in temperature within certain limits; positive geotropism, movement downward, may be brought about temporarily by mechanical shock, by salts and alkalies, by temperature changes (503, 689), to which, however, the animals may adapt themselves; with less constancy by increase in the density of the fluid containing them, and with lasting effect by lack of food. It has been suggested that the downward movement under these circumstances is protective, since it shields the animals from surface agitation of the water, from surface ice, and from failure of the surface food supply (500). We shall see that similar conditions often change the direction of an animal's response to light.

§ 49. Orientation to Gravity: *Cœlenterates*

Among the cœlenterates, geotropism is shown by certain hydroids, whose stems have a tendency to curve upward and their "roots" a tendency to grow vertically downward when the animals are placed in a horizontal position (714). The sea-anemone *Cerianthus*, whose normal position is head upward, will right itself if placed in any other position, though the righting reaction may be inhibited by contact stimulation on the side of the animal. It ordinarily lives with the body enclosed in a tube, and when taken from its proper habitat it seems to "prefer" a position, even horizontal, where the sides of the body are in contact with a solid, to a vertical position with its sides uncovered (424). The righting reaction of *Hydra* is not determined by gravity at all; the animal will take any position, vertical or horizontal, but "seeks" always to have its foot in contact with a solid (751 a). Some actinians have shown an interesting modification of gravity reaction through what we may call habit. Six specimens of *Actinia equina* were selected that had been fixed to the rocks in an "upside-down" position, that is, with the mouth end downward; and six others that had been right side up. In the first experiment all were placed upside down; the tendency to right themselves was decidedly stronger in those which had been previously erect. Similarly, when twelve selected in the same way were all placed right side up, the ones that had previously been in the reversed position showed a certain inclination to reassume it (258). On the other hand, the orientation of the polyp *Corymorpha palma* to gravity was entirely unaffected by keeping the animal for a long time in a position where it could not right itself; it assumed the upright position as soon as it was set free (714).

It was noted in the chapter on hearing that the peculiar organs occurring in certain Coelenterata and in many other animals, which were originally called otocysts because of their supposed auditory function, have had their name changed to that of statocyst since it has appeared that they subserve chiefly orientation to gravity. In jellyfish, removal of these organs does not seem to affect the animal's power of keeping its balance; apparently equilibrium is maintained here by the simple action of gravity, for dead jellyfish float in the right-side-up position (514, 521). It has been suggested that the statocyst organs are for the reception of stimuli produced by shaking, to which medusæ are apparently sensitive (521). Negative geotropism exists in *Gonionemus*, which swims to the surface of the water when disturbed (825). In ctenophors, the statocyst organ, which is usually at one pole of the body, has been found to function as an organ for the maintenance of equilibrium (741).

§ 50. *Orientation to Gravity: Planarians*

A good example of a specially developed reaction having for its result the "righting" of an animal in an abnormal position is offered by the behavior of a planarian that has been turned over so that its back rests on the surface of support. The reaction consists of a turning of the body, beginning with the head end, about the long axis, so that a spiral form is assumed. The dorsal surface of the animal is convex, the greatest thickness of the body being in the middle line. When the planarian lies on its back, it thus naturally tips to one side, like a keeled boat out of water. This side, being brought into contact with a solid, gives a reaction analogous to the negative one, that is, it extends or stretches. Such a stretching of one side when the

planarian is right side up would of course produce a turning in the opposite direction, a negative reaction. In this case, however, the opposite side does not contract to allow of turning, but maintains the same length. The necessary result is that the body is thrown into a spiral: as soon as the ventral surface of the head comes into contact with the solid, in consequence of the turning, the negative reaction of that end ceases. Thus the righting is progressively accomplished (561). The whole response can hardly be classed under the head of geotropism. Like that of *Hydra*, it is not made as the result of the pull of gravity, but is a reaction to contact stimulation; the animal will crawl in an upside-down position as readily as any other provided that the ventral surface and not the dorsal is in contact with a support.

§ 51. *Orientation to Gravity: Annelids*

Geotropism, in the marine worm *Convoluta roscoffensis*, has been found to fluctuate with the rise and fall of the tides, even when the animal is removed to an aquarium. In normal life the worms burrow in the sands at rising water, and come to the surface when the tide retreats. Prolonged exposure to air, or increase in the intensity of the light, causes them to move down the slope of the shore to moist places. These movements in the normal environment are represented by upward and downward movements of the animal when confined in a glass tube. Keeble and Gamble thought these oscillations in geotropism did not occur in darkness, and that the stimulus bringing them about was photic. When the summation of light stimuli passes a certain amount, they maintained, positive geotropism appears; when the after effect of light stimulation is dissipated, the

negative phase recurs (253). Bohn, however, finds that the oscillations do persist in darkness, and that their primary cause is the mechanical shock of the waves, as is further indicated by the observation that shaking the tube will cause the worms to descend (61). The geotropism of *Convoluta* is dependent on the statocyst (253).

§ 52. *Orientation to Gravity: Mollusks*

Among Mollusks, the slug has had its reactions to gravity carefully observed. When placed in a horizontal position on an inclined glass plate, these animals tend to turn either upward or downward, moving either with or against the force of gravity. Davenport and Perkins found that the same individuals differed at different times in this respect, and concluded that the sense of the geotropism was determined by obscure conditions. They also found that an inclination of only 7.5° on the part of the glass plate, representing only 13° of the full force of gravity, is sufficient to make the slugs orient themselves with reference to the pull of the earth, though the precision of such orientation increases as the angle increases (175). Frandsen thought it was the weight of the posterior part of the body that determined whether the movement should be up or down: that the natural tendency of all was to go downward, but that in some individuals the posterior part, which is poorly controlled, was heavier than the anterior, and pulled the animal around head upward (236).

Kanda (392, 393), on the other hand, thinks that in freshwater and marine snails the statoliths are the organs determining orientation to gravity, and that it is not merely passive: he claims to have observed that this orientation is most marked, the less the slope of the surface

on which the animal crawls. The response of *Physa*, a freshwater snail, to gravity depends in an interesting way on the animal's physiological condition: when the snail is in need of air it is strongly negative in its geotropism, crawling upward towards the surface of the water and disregarding all other stimuli: as soon as its lungs are full of air it is no longer sensitive to gravity (177). Buddenbrock (107, 108, 109) and Baunacke (29-32) have brought evidence to support the view that the statocysts in many mollusks are useful not so much in securing orientation to gravity, which is of little importance in such slow-moving animals, but rather in enabling them to right themselves, to direct their movements, and to dig in the sand. The statocyst organs in a cephalopod, *Eledone*, have been shown to function in maintaining equilibrium (249).

§ 53. *Orientation to Gravity: Echinoderms*

Righting reactions in the starfish have been described by Romanes (641). The tips of two or three rays are twisted around until the suckers in the ventral side have a firm hold of the supporting surface; the twisting is then continued, always in the same direction on the different rays, until the whole body is turned. Jennings (380) enumerates twelve different factors which determine which particular rays shall twist over and attach themselves first, but Moore (501) thinks that the "positive stereotropism," that is, the tendency to remain in contact with solids, of the tube feet is a sufficient explanation. It is not clear how a tendency to *remain* in contact with a mechanical stimulus can explain a tendency to *seek* such a stimulus when it is absent, and Jennings's view, that the original impulse to turn comes from the general state of unrest in which the

animal is thrown by its position, seems plausible. But what is the stimulus inducing the unrest? Not contact of the back with a solid object, for a starfish is not disturbed if its back is touched when it is crawling in the ordinary position; and not merely having its back directed downward, for it will crawl upside down on the under surface of rocks. Something abnormal about the stimulation of the tube feet when they are in contact, not with a solid support, but with the water flowing over them, must present the condition for the internal state of instability which occasions the twisting movements of the rays.

The sea-urchin, "a rigid, non-muscular, and globular mass," as Romanes calls it, with relatively feeble suckers, has a much harder time to right itself, and does not succeed in pulling itself over unless it is perfectly fresh and vigorous. It occasionally rests for some time when it has reached a position of stability halfway over, before continuing the process (641).

Lyon has observed marked negative geotropism in the larvæ of the sea urchin. He was unable to test Davenport's theory of the nature of the geotropic response by putting the animals in a solution of the same density as their own bodies, for the reason that such a fluid was too dense and sticky (being made of gum arabic and sea water) for them to swim in. That the response was merely a passive one he thinks improbable, because the larvæ from eggs that have been rapidly rotated, or "centrifuged," as it is called, have all the pigment on one side of their bodies and may therefore be supposed to have their ordinary balance disturbed; yet they rise to the surface just like the rest (450).

§ 54. Orientation to Gravity: Crustacea

That the statocyst organs in Crustacea are probably connected with equilibrium rather than with hearing we have already seen. Delage in 1887 found that *Mysis*, *Palæmon*, and other forms displayed serious disturbance of equilibrium when both eyes and statocysts were destroyed, showing that the eyes also play a part in the maintaining of balance (180). The eyes have been found to coöperate with the statocysts in the fiddler crab, *Gelasimus*, and also in another decapod, *Platyonichus* (127). Neither of these has statoliths. *Penæus membranæus*, on the other hand, was found to be permanently disoriented by destruction of the statocysts or even removal of the statoliths, while blinding produced no great disturbance, probably because of the animal's nocturnal habits (38, 250). Young crayfish with the statocysts destroyed will swim upside down as readily as right side up (111). But the prettiest evidence for the static function of the statocysts was obtained when powdered iron was substituted for the mineral bodies in the open statocysts of *Palæmon*. It was found that when a magnet was brought near, the animal would respond by taking up a position corresponding to the resultant of the pull of the magnet and that of gravity (407).

Specific righting reactions occur in many Crustacea, though in some cases these seem to be merely the incidental effects of ordinary locomotion. *Branchipus*, the fairy shrimp, normally swims upside down; if turned right side up when moving along the bottom of the vessel, it continues to move in this position without showing any disturbance until it happens to rise a little from the bottom, when apparently the weight of the body pulls it around into the usual upside-down position. The crayfish has two methods

of righting itself: a quick "flop" executed with the tail, and a slow and laborious raising of itself on one side and tipping over (179).

Many Crustacea show marked responses to gravity: for example, Parker found decided negative geotropism in the females of the marine copepods whose depth migrations he studied. It seems to be needed to counteract the tendency of the animals to fall to the bottom by their own weight (534). In certain copepods, light was observed to change the sense of the response to gravity, not by taking its place as a directive stimulus, but apparently by producing some physiological change in the animals. Their normal geotropism was positive, that is, they had a tendency to move downwards. In darkness, however, their geotropism became negative. They were also negatively phototropic to strong light. If, when in the negatively geotropic phase, they were illuminated from below by intense light, from which they would ordinarily have moved away, the change from negative to positive geotropism induced by the light was of sufficient influence to make them move downward toward it (210). Other facts regarding the relation of geotropism and phototropism are mentioned on pp. 209 ff.

§ 55. *Orientation to Gravity: Spiders and Insects*

Spiders and insects have no statolith organs. Bethe thinks that equilibrium is maintained in their case as a natural result of the position of the centre of gravity and the distribution of air in the body. He supports this view by experiments in which dead insects, allowed to fall through the air, assume the normal position, and is inclined to think that all animals without special static organs maintain their balance in this way (48). Negative geotropism in certain

insects, as evidenced by a tendency to creep from horizontal planes up vertical ones, was observed by Loeb (420). In light the eyes of insects have probably much to do with maintaining equilibrium. Certain aquatic insects, in experiments where the light was made to strike them only from below, as soon as they left the support on which they were resting, turned themselves upside down (622).

§ 56. *Orientation to Gravity: Vertebrates*

It has long been known that in vertebrates the static function resides in the ear, and especially in the semicircular canals (e.g. 103, 165, 229, 263). Various experimenters have noted that operations on the ears of fishes disturb the equilibrium of these animals. Sewall, indeed, found that section of the semicircular canals in the shark had no effect on its balancing powers, although operations on the vestibule and ampullæ did disturb movement (669); and Steiner got no effect on equilibrium from removing the contents of the labyrinth (692). Errors in method and observation probably influenced these results. Loeb found that severing the auditory nerve or removing the statolith from the dogfish caused the fish to incline toward the operated side and to roll the eyes in that direction (424). Total extirpation of one labyrinth in the perch was observed by Bethe to make the fish curve toward the affected side. The fish *Scardinius* showed a tendency to curve toward the opposite side (48). Lee's experiments on the dogfish showed a very definite relation between the position of the canal operated upon and rolling movements of the fish. Cutting the front canals caused the fish to dive forward, cutting the rear canals made it dive backward, and cutting the canal on either side made it roll over toward that side. A natural

explanation of this behavior is to suppose that the absence of stimulus from the cut canal produces the same effect that rolling the fish in the opposite direction, and thus diminishing the pressure of the fluid in the canal, would produce. The fish "feels as if" it were being rolled over, and makes movements to regain its equilibrium. When the nerves supplying the ears on both sides were cut, the fish became perfectly indifferent to its position and would float upside down without any effort to right itself. The vestibule and otoliths of the fish ear are thought by Lee to be concerned with static equilibrium; that is, with the maintenance of position while the fish is at rest, while the canals are concerned with balance during motion (dynamic equilibrium) (416). It may be added that experiments on the sea horse indicate that destruction of the labyrinths in this animal has no effect on equilibrium: the upright attitude is due to the position of the air bladder and is assumed even by dead animals (251).

That vision may materially aid in maintaining equilibrium in vertebrates is indicated by evidence from various sources, among others, the observation of Bigelow that goldfish in which the nerves supplying both ears had been cut recovered after two or three weeks and could swim quite normally except when they were placed in a large body of water and made to swim rapidly, when they showed no power of preserving their balance (54). Their successful performance of slower movements was very likely due to the use of sight.

Sensory impulses from the body muscles themselves undoubtedly cooperate with those from the semicircular canals in the maintenance of balance. They are evidently involved in the peculiar withdrawing movements by which land animals, even puppies, kittens, and young rats whose

eyes have not opened, save themselves from falling when they reach the edge of the object on which they have been crawling (490, 683). Water-dwelling animals, accustomed to plunge off solid supports, lack this protective instinct; Yerkes showed that among several species of tortoises, some land-dwelling, some amphibious, and some aquatic, the first mentioned were much more reluctant than the second to crawl off the edge of a board, and the second more reluctant than the third (810).

§ 57. *The Psychic Aspect of Orientation to Gravity*

Glancing back over these examples of the responses made by animals to gravity, we note that while in some cases the earth's attraction appears to act mechanically upon the animal, causing the body passively to assume a certain position, the common method of bringing about orientation seems to be that some structure in the body, placed in an abnormal position, presents a stimulus which brings about a compensatory movement. This structure may be heavier particles of the body substance, as probably is the case in *Paramecium*; it may be a statolith, or the fluid in the labyrinth; it may be the eyes. In any case, what shall we say about the sensation quality involved? Perhaps the reactions produced are wholly reflex. Perhaps the statolith or the canal fluid produces a specific sensation quality. Or perhaps, as Verworn thinks, the sensation quality is merely that of pressure (741). Whatever its nature, spatial perception, the perception of the spatial relations between several stimuli simultaneously apprehended, plays no part in the orientation of animals to gravity.

§ 58. Orientation to Light

In some animals light is sought or avoided not simply because of the fact that in certain intensities it stimulates to restlessness and activity (photokinesis), so that they come to rest in regions illuminated by other intensities; but through a direct movement of the animal towards or away from the source of light. It is this type of response to which Loeb and his followers restrict the term "tropism." Plants show it, both in the orienting of their stems with relation to light, and in the movements of their freely swimming "swarm spores." In the case of animals, it is illustrated by the behavior of the sea-anemone *Actinia cereus*. Weak light causes expansion of the tentacles of this organism perpendicularly to the light rays. If the light is increased, Bohn (86) says the tentacles "tend to orient themselves in the direction of the rays, and finally converge in a bundle parallel to that direction," a response which has the effect of protecting them from the intense light. Again, the tube-dwelling worm *Spirographis spallanzanii* gradually curves its tube until its mouth end faces the direction from which the rays of light come, and another marine worm, whose tube is absolutely stiff, adapts itself to a change in the direction of the rays by curving the newly formed portions of the tube as it constructs them (422).¹ Sea-anemones and tube-dwelling worms closely resemble plants in their mode of living. In freely moving animals, where the oriented movement is made in response to light, it is commonly preceded by body orientation; that is, the body first faces or turns tail to the light, and the animal then moves forward. Sometimes, however, there is no regular body

¹ Hargitt (288) finds no such constancy of orientation in *Spirographis* as would warrant Loeb's calling the motion a tropism.

orientation; the animal moves, for instance, always away from the light, which means that it moves forward if its body happens to be oriented with the tail to the light, or backward if its head happens to be directed to the light. Such behavior is reported by Holmes of mosquito larvæ (338) and by Gee of leeches (257). On the other hand, Hadley (274) says that young lobsters always orient with the head towards the light, though they may move either away from or towards it. In some animals with eyes, such as the crustacean *Daphnia*, there is reason to think that body orientation is primarily an affair of eye-orientation or fixation. This at least is the view of Rádl (621). He placed *Daphnia* under a microscope in such a way that only the eyes could be moved. When the light coming from below was diminished, the eyes rolled upward; when the light coming from above was diminished, the eyes rolled downward. Holmes (330) observed that in amphipods, blackening one eye of a positively phototropic animal causes a turning toward the blackened side, as if the animal were trying to restore the missing illumination; similar experiments upon negative animals produced turning towards the other side.

It is the view of Loeb (434) that oriented response of animals to light is wholly analogous to the same type of response in plants. Since plants with their very slow and limited movements are subject more to light as a continuous stimulus than to sudden changes in light intensity, orientation in their case must be brought about by the steady and continuous action of the light. Accordingly, Loeb maintains the view that the tropism or oriented response of animals to light is dependent on the continuous action of the light, and not on changes in light intensity. It is thus a mode of response that has nothing in common with "sen-

sibility to difference," which Loeb recognizes as an independent form of reaction. In support of his continuous action theory Loeb lays great stress on the proof, by the botanist Blauuw, that the "Bunsen-Roscoe Law," that is, the law that the effect of weak light acting a long time is equal to that of strong light acting a short time, holds for plants; Loeb thinks it holds also for animals.

The action of continuous light in producing a tropism has been explained in two ways: (1) as the effect of the direction of the light rays traversing the animal's body, and (2) as the effect of having symmetrical points on the animal's body stimulated with unequal degrees of intensity. In his earliest discussion of the subject, Loeb (419) expressed himself positively in favor of the former hypothesis. "The orientation of animals to a source of light is, like that of plants, conditioned by the direction in which the light rays traverse the animal tissue, and not by the difference in the light intensity on the different sides of the animal." Bohn, in general the ardent follower of Loeb, urged as a "fundamental objection" to this that "the 'luminous rays' which strike a living body have, save in wholly exceptional cases, various directions, being reflected, diffused, and refracted by neighboring bodies" (80). Moreover, the animal bodies which are opaque could not be traversed by light rays. Loeb seems later to have abandoned the "direction theory" of the tropism. The "intensity theory" was first proposed by Verworn (743).

How can differences in the intensity of a stimulus falling upon symmetrical and opposite points on an animal's body bring about orientation? Let us call the two points a and a' , a being a point on the right side of the animal's body and a' a symmetrically placed point on the left side. Suppose the animal has a tendency to orient itself

positively to the light, that is, turn towards the light, and suppose a ray of light strikes it obliquely from the right. Evidently the point *a* receives a greater intensity of the stimulus than the point *a'*. Now if the animal is positive to light, Loeb would suppose that its chemical constitution is such that light causes, either by direct action on the muscles or reflexly through the eyes, a contraction of the muscles. Hence the muscles at point *a*, or controlled through point *a*, would contract more strongly than those at point *a'*: the animal in consequence would turn towards the right, that is, towards the light, and would continue so turning until the light struck *a* and *a'* with equal intensity, that is, until it directly faced the light. All subsequent movement would have to be directed straight towards the light. If the animal is negative in its response to light, then it is so chemically constituted that light causes a relaxation of the muscles. In such a case, the point least strongly stimulated would produce the strongest muscular contractions: the animal would turn towards that side, and would continue turning until opposite points were equally stimulated, that is, until it headed directly away from the light: all subsequent movement would have to be in this direction.

Now Jennings (373), has suggested that the oriented reactions of certain organisms, at least, are really due to changes in the intensity of the light, brought about by the animal's own movements. This view would, if generalized, put all directed light reactions in the "sensibility to difference" class given to changes in intensity: the effect of continuous light would be limited to photokinesis. Let us see how an oriented response may be conceived to result from reactions to changes in light intensity. In the Protozoa, according to Jennings (373) and Mast (463), the orientation is

due to negative reactions given when the organism in its ordinary swimming movements, which usually involve turning from side to side, either passes into a region of greater or less illumination, or swings its anterior end "toward or away from the source of light, so that it is shaded at one moment and strongly illuminated at the next." Suppose, that is, an animal makes in its locomotion slight random movements of the head from side to side. Suppose that one side of it is more brightly illuminated than the other. If the animal is positive to light, it has the characteristic of making a negative response whenever its head end is suddenly darkened. This will happen when the head end is accidentally turned away from the light; consequently all such random movements will be checked, while random movements of the head towards the light will not be checked. Hence the animal will turn until its head points towards the light: in this position random movements towards either side will be equally checked because they will equally tend to bring the head into a darker region; and so movement will take place in a line generally towards the light, though still with balanced random movements to either side. If the animal is negative, it has the characteristic of making negative reactions when the illumination of the head is suddenly increased, and obviously this will bring about orientation with the head end away from the light.

In *Volvox* (see page 136), orientation is held by Oltmanns (528) and Mast (464) to occur after this fashion. The reaction of a *Volvox* colony, which in moderate light is positively phototropic, takes place in consequence of a response by each individual in the colony given when, as the colony rotates, that individual passes from a higher to a lower intensity of light.

A point which has been regarded as of much importance in deciding between the theories of Loeb and Jennings on orientation to light is the actual occurrence or non-occurrence of random movements. Thus Holmes (334) believes the negative orientation of earthworms to light occurs by the checking of random movements of the head towards the light. In the crawling movements stimulated when light is thrown upon the worm, the head is turned from side to side. If it happens to be turned toward the light, it is withdrawn. Holmes explains the observation of Parker and Arkin that the head of the worm is much more apt to turn from the light than toward it (552), by saying that account was probably taken here only of the first decided turn made. He himself experimented by lowering a worm, crawling on a wet board, while its body was in a straight line and contracted, into a beam of light at right angles to the body, and noting the first movement of the head. This was found to be twenty-seven times away from the light and twenty-three times toward the light. A similar method of orientation by "trial and error" was observed in the leech and in fly larvæ by Holmes (334).

E. H. Harper, on the other hand, working on the earthworm *Perichata bermudensis*, declares that if the light is strong enough there are no random movements of the head at all, but the first movement is a direct reflex away from the light. When the light is only moderate, the appearance of random movements is due to the fact that the worm is less sensitive in a contracted than in an expanded state. Locomotion consists in a series of contractions and expansions, and "as each extension begins in a state of lower sensibility, the anterior end may be projected toward the light, only to be checked when its increase of sensibility with extension makes the stimulus appreciated" (288).

A similar suggestion that orientation may occur either by a definite reflex or as the outcome of random movements, according to the animal's physiological condition, is to be found as early as the work of Pouchet on fly larvæ. He noted that the courses taken by the larvæ were either straight, "or they present to right and left indentations due to the wavering movements which the animal makes . . . in a certain number of cases, as if to take at each instant a new direction." These individual differences might have been accounted for, says Pouchet, by differing degrees of hunger in the larvæ (614). Herms (296) reports that to low intensities sarcophagid flies orient by random movements: while to high intensities they orient directly. Bittner, Johnson, and Torrey (58) find that the earthworm orients to light without any random movements. Hadley (274) finds the same true of larval lobsters, Crozier (159) of a holothurian, and Bancroft (16) reports of *Euglena*, a protozoön which has the spiral method of swimming characteristic of so many animals in this group, that "there is nothing of trial and error here: the organism orients as definitely as its spiral locomotion will allow."

When the "direction theory" of the tropism was receiving more attention than at present, evidence that an animal oriented in response to the direction of the light rather than to the comparative intensity of stimulation on symmetrical points was taken as arguing against Jennings's view of the tropism as a response to changes in light intensity produced by random movements. Attempts were made to demonstrate the direction theory experimentally. A typical experiment of this type was that of Strasburger (695), made long before Jennings's views were in the field, upon the swarm spores of certain plants. He placed over the vessel containing them an India ink screen, thicker at one

end so as to cause gradations in the intensity of the light reaching the vessel. When the light fell perpendicularly through this screen, the distribution of the swarm spores through the vessel was nearly uniform; that is, the differences of intensity had no effect. When the screen was removed, and the light fell at an angle, the spores immediately oriented themselves to its direction, and preserved this orientation even when the screen was replaced. They would move toward the light even when by so doing they passed into a region of less intense illumination. Jennings suggested that these results were due to the fact that "turning the sensitive anterior end away from the source of the light" would diminish the effective illumination of the animal more than passing into a slightly less illuminated region. That is, the two ways of changing the intensity of the stimulus, moving forward into a darker region, and turning the head end away from the light, are here opposed: the latter effect is stronger than the former, hence the organisms make the negative reaction when the head end is turned from the light, and move toward the shaded region. "If the difference in intensity of light in different parts were increased till the change in illumination due to progression is greater than the change due to swinging the anterior end away from the source of light, then the positive organisms would gather in the more illuminated regions" (378, page 148).

§ 59. *Influences Affecting the Sense of Light Orientations*

In no class of animal responses to stimulation is the effect more dependent upon the coöperation of a number of conditions than in those involving orientation to light. Many influences have been found to reverse the sense of light re-

actions, transforming negatively phototropic into positively phototropic animals, and *vice versa*. That such reversal should occur in response to increase or decrease of the *intensity of the light* is what one would naturally expect; if a certain intensity of illumination is favorable to the life processes of an animal, it would seem appropriate for it to seek light of that intensity but avoid light of greater intensity. Many animals, like *Gonionemus*, are positive to light of moderate intensity and negative to strong light (802). The females of the crustacean *Labidocera* migrate to the surface of the water at nightfall because, like the earthworm, they react positively to faint light; and move downward at sunrise because they are negative in their response to intenser light (534). On the other hand, Holmes observed that *Orchestia agilis*, an amphipod crustacean, would, if brought from strong to weaker light, become negative for a short time; the meaning of such a change it is difficult to conjecture (330). Sudden reduction of light causes a temporary negative phase also in *Convolvula roscoffensis* (253).

Prolonged action of light may alter phototropism: the "depth migrations," that is, the periodical movements toward and away from the surface of the water, in the free-swimming larvæ of the barnacle, *Balanus*, are due apparently to the fact that an exposure of several hours of light will make positive animals negative, even though the light at the end of the period of exposure is decidedly fainter than it was at the beginning (269). The positive reactions of the water insect *Ranatra* increase in violence the longer the light acts; on the other hand, after being kept in darkness for several hours, *Ranatra* is negative on first being taken out (335). *Daphnias* kept in darkness for a time become decidedly negative to diffused daylight,

whereas if kept in light they would have been positive. A sudden change in light intensity, either brightening or darkening, has the effect of making positive *Daphnias* temporarily negative (532).

Temperature changes influence response to light. The obvious suggestion here would be that since increased temperature often accompanies increased intensity of light, animals that are positively phototropic only up to a certain degree of illumination ought to become negative when the temperature is decidedly raised. This, however, is by no means always the effect produced by increased temperature. Strasburger's swarm spores became positive in higher temperatures, negative in lowered ones (695). *Orchestia agilis*, which we have just seen becomes temporarily negative on being brought from strong into weak light, may be made positive again if the water is slightly warmed. When the same animal is dropped into water, it becomes strongly negative, but it will show a positive response if the water is heated almost to a fatal point (330). Essenberg (209) finds that certain aquatic insects are more strongly positive when the temperature is increased. On the other hand, the copepods and annelid larvæ studied by Loeb were made negative by increased, positive by lowered, temperature. Other crustaceans, e.g. *Daphnia* (808, 185), had their responses to light unaffected by a fairly wide range of temperature changes.

Increasing or decreasing the density of the water will also affect phototropism. In some copepods diluting the water produced negative responses to light, while increasing its density brought about those of the opposite sign (425). Diluting the water produced negative phototaxis in the larvæ of *Palæmonetes* (451). Parker failed to find any such effect in the case of the copepods studied by him (534).

W. Ostwald has called attention to the possibility that "internal friction" between the organism and the medium may affect various tropisms. Freshly caught *Daphnias* which are negative or indifferent, quickly become positive if gelatine or quince emulsion is added to the water. Since they would become so in time anyway, Ostwald thinks the mechanical friction of the sticky liquid simply acts as a "sensibilator" and brings on this positive phase sooner (532).

Change in the purity of the water also sometimes produces change of sign in the response to light. The amphipod *Jassa*, negative in ordinary sea water, becomes positive in foul sea water (330). The *presence of chemicals* is an influence probably identical with the one just mentioned. Various Crustacea have had the direction of their reactions changed by carbonic or other acids, ammonium salts, ether, chloroform, paraldehyd, and alcohol (430). Acids and salts will reverse the responses of May fly larvæ (794). The ultra-violet rays will make positive *Balanus* larvæ temporarily negative and have a similar effect on *Daphnia* (502).

The state of hunger or satiety in an animal must be reckoned with: the caterpillars of *Porthesia*, for example, are decidedly positive when hungry, much less so when fed (423). The slug *Limax maximus*, ordinarily negative to strong light, is positive to light of any intensity when hungry (236).

Mechanical stimulation is most striking in its effect on light reactions. Pouchet in 1872 noted that fly larvæ after having been shaken fail to display their usual orientation to light (614). The copepod *Temora longicornis*, usually negative, can be made positive by shaking it (425). Very curious phenomena of a similar nature have been observed in the case of some Entomostraca. Certain individual

specimens of the ostracod *Cypridopsis* appeared to be decidedly positive, others negative. Careful experimental analysis of the conditions revealed the following as the true state of affairs. The animals are predominantly negative. But contact with a mechanical stimulus has the effect of making them positive; thus a negative animal that is picked up in a pipette, or merely comes in contact with the end of the trough in swimming away from the light, may become positive. In course of time such a positive animal will become negative of its own accord, so to speak, without further mechanical stimulation, but such stimulation, if applied, makes it negative at once (718).

Similar experiments upon *Daphnia* and *Cypris* gave results of the same general character. The strong positive tendency of the former may, by several times taking the animal up in a pipette, be made very temporarily negative; the opposite effect could not be well tested because of the difficulty of preserving the negative state long enough to experiment on it. In the case of *Cypris*, an individual temporarily negative could be made positive by picking it up, but the positive phase could not be similarly reversed. No other sudden stimulus produces the effect which is thus induced by mechanical contact (800).

The effect of contact was observed by Holmes in the terrestrial amphipod *Orchestia agilis*. The most permanent phase of these animals is positive, although they are at rest under seaweed on the beach by day. But when they are thrown into the water, they become strongly negative, no matter what the intensity of the light; and to a considerable extent this effect is independent of the temperature (330, 106). In the case of the copepod *Labidocera aestiva*, being picked up in a pipette will make the females, ordinarily positive, negative for a time. The males are normally

slightly negative, but picking them up, instead of reversing this tendency, increases it (534). The strong positive phototropism of the "water scorpion" *Ranatra*, an hemipterous insect, may be made negative by handling, and especially by dipping in water (335).

Periodical changes in the sense of response to light have been observed in animals subjected to periodical changes in environment. The gasteropod mollusk *Littorina* lives on the rocks of the seacoast in regions where it is covered with water at high tide and exposed to the air at low tide. According to the height at which they are found, some of these animals undergo the alternations of wetness and dryness at the ordinary tidal periods, twice a day, while others are reached by the water only at the special high tides occurring every fourteen days. Mitsukuri showed that when the waves of a rising tide cover these mollusks, they display negative phototropism and seek shelter in rock cavities; while as soon as they are again exposed to the air, their phototropism becomes positive and they emerge in search of food. Further, he found that a *Littorina* whose phototaxis was negative could be made positive by being subjected to the action of a stream of water for a time (496). Bohn later studied the effects of placing black or white screens near the animals at various angles to their crawling movements, and found that the black screens exerted an attractive influence at certain times, the white screens at others. These changes in the "sense" of the phototropism correspond in time to the oscillations of the tide, even though the animals are studied in the laboratory; they tend gradually to grow less pronounced, however, under such circumstances. Further, the level from which the *Littorinas* are taken influences the nature of their response to light. Those from high levels, "which undergo pro-

longed and intense desiccation, habitually move following the direction of the luminous field in the negative sense; the Littorinas from low levels, which undergo only short and slight desiccation, move, habitually, following the direction of the luminous field in the positive sense." The former become positively phototropic at the time of highest water, the latter negatively phototropic at the time of low water. In all cases, the tendency is for the animals to become negative at low-water time. The attraction of the dark screens represents that of the dark surface of the rocks (80). Similar oscillations corresponding to the periodicity of the tides were observed in the annelid *Hedista diversicolor* (80), in the sea-anemone *Actinia equina* (65), and in the hermit crab (192, 194).

It is probable that such rhythmic changes in the sense of light response are due to the effect of a rhythmically recurring cause, such, for instance, as the mechanical disturbance caused when the waters of the rising tide begin to agitate the pool in which the animal dwells, or to the wetness or dryness of the tissues. Bohn has suggested this explanation for the oscillation of *Hedista*, just mentioned. He supposes that when the annelid is dry, light has the power of exciting muscular movements, that is, a kinetic effect. This means that when the worms have accidentally crept into the shade they come to rest. If one eye has its illumination diminished, there is an inhibition of muscular activity on that side, and consequently a turning in that direction. At the period of high tide, when the muscles are wet, the action of light on the animal is inhibitory and the above phenomena are reversed (80). Heat and dryness make terrestrial amphipod crustaceans positive to light; cold and wetness make them negative (106).

The state of rest or movement is still another factor. The

"mourning cloak" butterfly, *Vanessa antiopa*, on coming to rest in bright sunlight, orients itself with the head away from the light. When it moves, on the other hand, it flies toward light of any intensity (537). Bohn also has noted that certain butterflies orient themselves when alighted in such a way that the posterior part of the eyes is toward the light. When in this position there is a tendency for the wings to be spread apart, while when the insect is facing the light the wings are closely folded (82). The effect on the wings was noted in *Vanessa* also, and, it is suggested, may have some function in bringing the sexes together (537). The pomace fly when at rest is not oriented at all. Light exerts upon it merely the effect of stimulating it to movement, a kinetic, not a directive, effect. When the movement has been started, however, it is directed toward the light. But owing to the kinetic influence of the light, when the insects have been long exposed to sunlight they tend to come to rest in the more shaded portions, with their heads away from the light, for this is the position in which they are least stimulated to movement. The kinetic effect increases with the intensity of the light, but its directive effect, through which orientation is secured after the movement is started, was at least in one case lost under intense light (116). Brundin (106) has suggested that the effect of mechanical stimulation in reversing light reaction may be due to the state of activity it induces.

The *background*, finally, sometimes determines the sense of the reaction. Keeble and Gamble found that while the crustacean *Hippolyte varians* would move toward the light whether it was on a white or black background, *Macromysis inermis* was negative on a white ground and positive on a black ground (396).

§ 60. *The Psychic Aspect of Orientation to Light*

The behavior of an organism which, by the unequal contraction of symmetrically placed muscles, is forced around into a position directly facing or turning tail to light, the light acting as a continuous stimulus and not through changes in intensity, is without any parallel in human experience, and hence suggests no psychic accompaniment. Yet there seems to be a considerable amount of evidence that such a type of reaction does occur, given the proper amount of stimulus and the proper physiological condition in the animal. It is a fact of much interest, however, that when we reach organisms beyond a certain point in the ascending scale of complexity, the tropic type of response to light begins to give place to more variable responses suggesting analogies with our own behavior. The individual experience of an animal strongly modifies its tropisms, as we shall see in a later chapter. Brundin (106) says that in certain amphipod crustaceans which he studied, the "mode of behavior exhibits a transition from the stage at which the creature is at the mercy of its environment to a stage at which it is beginning to hold its own against the forces which have shaped it." Quite possibly, however, the ability to modify tropic response by individual experience is found in all animals, and not merely in those above a certain stage; it does seem to be true, though, that the tropisms are more readily overthrown by other influences, the higher the animal. Thus Holmes (337) says of fiddler crabs that phototropism is easily overcome by fear; although they are strongly positive they will run away from a moving light. "Light," he says, "is followed much as an animal pursues any other object of interest"; and Turner (728) has made similar com-

ments on the behavior of certain insects to light. Bohn says of the mollusk *Littorina* that when its tissues are neither very wet nor very dry, it ceases to respond with a fatal necessity to light; "the animal seems, as it were, to disengage itself from the influence of external forces, seems no longer to behave like a pure machine: it goes to the stones and seaweed where it may find shelter and nourishment as if it saw and was conscious of them" (80).

§ 61. *Mutual Influence of Light and Gravity Orientations*

Orientation to light and orientation to gravity are not without mutual influence in determining the behavior of an animal. Supposed instances of this have been noted in the case of the periodically changing geotropism of *Convoluta roscoffensis* (253) and in the copepods observed by Esterly (210). The relations of gravity and light responses in the larvæ of the squid, a cephalopod mollusk, seem to be as follows. The larvæ have a tendency to rise to the surface of the water both in darkness and in light, suggesting negative geotropism. Two test tubes were arranged by Loeb, one lying horizontally and at right angles to a window, the other inclined at an angle of 45 degrees from the upright position, and with the upper end directed away from the window. Larvæ were placed in both tubes; those in the former showed positive phototropism by collecting at the end nearest the window, but those in the latter gave evidence that their negative geotropism was stronger than their positive phototropism by rising to the upper end, although it was farthest from the source of light (428). It is not usual for geotropism thus to come off victorious in a contest with other tendencies. Jennings says, "As a general rule the reaction to gravity is easily masked by

reactions to other stimuli" (378, p. 150). In the mollusks observed by Bohn, the tendency in ascending or descending the rocks is to orient the body in the line of the greatest slope. When light and gravity are acting together upon the animal, its movement seems to be a resultant of the two, but if the mollusk is made to move on a vertical plane, gravity thus exerting its maximal force, the influence of the light disappears altogether; and if the animal is put in an upside-down position by further tipping of the surface, the sense of its phototropism is reversed; that is, it may be repelled instead of attracted by a dark screen (80). The fairy shrimp, *Branchipus*, is positively geotropic in light, negatively geotropic in darkness (454).

A curious tendency has been noted by many observers in insects with both eyes blinded; namely, to fly straight up into the air. Forel thought they did so because in no other direction could they escape obstacles (231); but this fact they would have to learn by experience, for which, in some cases at least, they do not take time. Plateau believed the rising into the air was due to sensations produced by the action of the light on the surface of the body, leading the insects in the direction of the strongest light, which usually comes from above. He supported this view by showing experimentally that a blinded insect would not rise if set free at night, while on the other hand, if liberated in a lighted room, it would, in spite of the blinding, fly toward the light or the lightest part of the ceiling (596, 599). In the butterfly *Vanessa*, Parker thinks the rising due to negative geotropism, as the insect flew upward in a darkened room (537). Axenfeld suggested that it might be caused by light penetrating the integument of the head (9).

§ 62. *Orientation to Other Forces*

One force, which, as was noted in Chapter III, produces orientation, namely, the electric current, we shall leave out of account. It is not a stimulus to which animals are normally subject, and though its action on living matter is of great interest to the physiologist, the comparative psychologist's difficulty in finding a psychic interpretation for the facts may justify setting them aside. Similar considerations apply to orientation to centrifugal force. There remain the orientations that have been termed respectively "rheotropism" and "anemotropism," responses to currents of water and to currents of air.

The tendency shown by many aquatic animals to orient themselves with head up-stream, and to swim against the current, was formerly thought to be a response to the pressure exerted by the current — a reaction leading the animal to resist pressure. Lyon, however, pointed out that this explanation assumes rheotropism on the animal's part. It is because the animal opposes the current that the current exerts any pressure. If it merely allowed itself to be carried passively along, and if the current surrounding the animal flowed with uniform velocity in all its parts, no stimulus whatever could be exerted by the water pressure (448). It seems probable that eyeless animals do not, as a matter of fact, orient themselves against a current of this sort, and that rheotropism in their case occurs when a current of unequal velocity disarranges their movements, or when they are in contact with a solid body. Thus Jennings has suggested that in *Paramecium* the reaction is due to the fact that unless the animal has its head to the current, the flow of the latter will interfere with the normal backward stroke of the cilia, causing

negative reactions until the disturbance is removed by proper orientation (378, p. 74). In animals with eyes, however, there is reason to think that apparent rheotropism is largely an affair of vision. Lyon's theory of rheotropism in fishes is that the fish orients itself and swims in such a way that its surroundings, the bottom of the stream, for example, shall appear to the sense of sight to be at rest, an hypothesis which, as we shall see, was adopted by Rádl to explain the "hovering" of insects in one place (622). Lyon supports it by experiments where the bottom or sides of the aquarium were caused to move in the absence of any current in the water, and the fish was found to follow them. When the fish was placed in a revolving glass cylinder, it followed the revolutions, although there was a slow current, of course, in the same direction, against which, on the pressure theory, the fish should have moved. Still more decisive was the experiment where young fish were placed in a corked bottle full of water which was submerged and put near a wall covered with algæ. When the bottle was moved in one direction, all the fish went to the opposite end, although no current could have been produced. Again, a wooden box with ends of wire netting, the bottom covered with gravel and the sides with seaweed, was used; fish (*Fundulus*) were placed in it, and the box was held lengthwise in a strong current. The fish oriented themselves, but as soon as the box was released and allowed to float away, they lost their orientation, though their relation to the current was in no way altered. Blind fish, Lyon found, oriented themselves by touch, sinking to the bottom. There does, however, appear to be, in some cases, a genuine pressure reaction to current, for when water is rushing through a small hole into a tank containing blind fish, they keep their heads to the current

without touching anything. Here the different parts of the stream have different velocity, and pressure stimuli are actually applied to the skin. There must be pressure reaction, also, when fish actually swim up-stream instead of merely maintaining their places against a current (272). Such a reaction was displayed, probably, by some shrimps which, being in the water with the fish in the revolving tank experiment, did swim against the current instead of with it (448).

Some very interesting behavior touching on this same point was observed by Garrey in a school of the little fish called sticklebacks. He noted that if any object was moved along the side of the aquarium containing them, the whole school would move along a parallel line *in the opposite direction*. If an individual fish happened to be heading directly toward the object, it would turn in the *opposite* direction from the one in which the object was moved; if it was heading somewhat in the opposite direction already, it would turn farther in that direction until parallel with the object's line of motion; if it was heading somewhat in the same direction as the object, it would "back off hesitatingly," and reverse itself by a turn in either direction, usually taking the way around toward which it was already partially headed, if the object was rapidly moved, but the other way around if the object's motion was slow. At first sight this behavior seems to display an instinct precisely opposite to that of keeping the visual field constant. Yet the sticklebacks, when placed in a cylindrical glass tank inside of a black and white striped vessel, moved with the latter when it moved, proving that they possessed the usual tendency shown by Lyon to be involved in rheotropism. Garrey points out that movement in the opposite direction is produced not

when the whole visual field moves, but when it is at rest, and one object in it moves. Can it be, he asks, that the moving object "fixes the attention" of the fish and produces an apparent motion of the background in the opposite direction, which motion the fish follows? (254.)

Rheotropism in water arthropods may be similarly accounted for, and in the opinion of Rádl, this same tendency explains the habit swarms of insects have of hovering over the same place, a phenomenon which Wheeler thought might be due to odors emanating from the soil (780). Insects will often be found to follow an object over or under which they are grouped in the air, if it be moved (622). Swarms of insects may be noted in the air over a country road, following its windings and apparently oriented by the contrast between the road and the dark banks on either side. When, however, resting insects turn so as to keep their heads to the wind, the reaction is evidently really due to the wind and not to their visual surroundings (646). Probably the disturbance to their wings produced by any other position causes them to rest only in the "head-on" orientation.

The responses of animals to different intensities of *heat* seem not to involve a definite orientation of the body. A temperature above the optimum produces wandering movements, which cease when the animal happens to reach the proper temperature (480, 483, 808).

CHAPTER IX

SPATIALLY DETERMINED REACTIONS AND SPACE PERCEPTION (*continued*)

§ 63. *Class III: Reactions to a Moving Stimulus*

SPECIALIZED response to a stimulus in motion, that is, one which successively affects several neighboring points on a sensitive surface, is also frequently met with in animal behavior. Its usefulness is obvious: a stimulus in motion is very commonly a living creature, hence either an enemy or food. In any case it must be reacted to with extreme promptness. Reactions of this class may be distinguished as tactile or visual according as the moving stimulus is mechanical or photic.

We find good examples of specialized reactions to *motile touch* in the coelenterates. The sea-anemone *Aiptasia* gives its most violent reaction, involving all the tentacles at once, when touched by a moving object (521). The medusa *Gonionemus* makes, in the case of a moving mechanical stimulus, its single exception to the rule of responding by the feeding reaction to edible substances only. The tentacles are wound corkscrew fashion about a glass rod drawn across them, they bend in toward the mouth, and the bell margin bearing them contracts; the feeding reaction goes no further, however. But the response is differentiated from that to any other form of stimulation by its greater speed: the reaction time is from .3 to .35 of a second, compared with .4 to .5 of a second for other stimuli

(802). Special vigor and speed generally characterize reactions to contact with moving objects. In eliciting the scratch-reflex of dogs, an object drawn along the skin is decidedly more effective than one pressed against the skin for the same length of time (681, p. 184). The physiological effect is probably, Sherrington says, the same as that involved in the "summation" of successive slight stimuli applied at the same point. As is well known, the latter will bring about a response of considerable violence, though each stimulus acting alone would apparently be without effect.

Is it likely that these responses to moving stimuli in contact with the skin involve the perception of movement as a form of space perception; that is, a perception of the successive positions occupied by the stimulus and their relative direction? I think we may say that they probably do not, in the lower animal forms at least. And a chief reason for saying so lies in the fact that the reactions are so rapid. To perceive the spatial relations of stimuli, or any other relations, is a process not favored by great speed of response. The quicker the reaction, the less clear the perception of its cause: such seems to be the general law. The sensation accompanying contact with a moving object may differ in intensity from that accompanying a resting stimulus; it may, in the lower forms, differ qualitatively in some way not represented in our own experience, but it can hardly be connected with the more complex psychic processes involved in any form of space perception.

In vision, also, there are special arrangements for reacting to moving stimulation. The sensitiveness of many animals to changes of light intensity, although not a direct adaptation to the spatial characteristics of a stimulus, serves the same purpose, for changes in light intensity are oftenest

brought about by objects in motion. In the mollusk *Pecten varius*, a transition from shadow vision to movement vision is illustrated: the animal closes its shell when a shadow is moved so as to fall on its eye spots in rapid succession (628). Generally speaking, the simple invertebrate eye, however, is adapted to respond to changes in light intensity rather than to moving objects. Plateau found that caterpillars, which have only simple eyes, could see moving objects no better than those at rest (597), and Willem was inclined to think snails saw resting objects better than moving ones (788). On the other hand, the compound eye (see page 219) is specially formed to be affected by moving stimuli. The crayfish will react to anything of fairly good size in motion, but is apparently unable to avoid stationary objects in its path (40). The poor vision of the compound eye for resting objects is shown by the ease with which insects may be captured if the movements of the captor are very slow. They may be readily approached, also, if the movements are all in the line of sight, that is, directly toward the insect, so that successive facets of the compound eye are not affected, as would be the case in lateral movements. Let the reader try bringing the hand slowly straight down over a fly, and see how much closer he can come before the fly is disturbed than he can if the hand is moved from side to side. Plateau, from experiments on different orders of insects, concludes that "visual perception of movement" is best developed in the Lepidoptera (moths and butterflies), Hymenoptera (ants, bees, and wasps), Diptera (flies), and Odonata (dragon-flies); that the distance at which movements can be seen does not exceed two metres, and averages 1.5 metres for diurnal Lepidoptera, 58 cm. for Hymenoptera, and 68 cm. for Diptera (599).

It is possible that response to a moving stimulus received

through the eye may be accompanied by spatial perception of movement, although if the eye is compound, the experience must differ from our own visual movement perception.

§ 64 *Class IV: Reaction to an Image*

By an image is meant the perception of simultaneously occurring but differently located stimuli as having certain spatial relations to each other. Through its means, or that of the nervous processes underlying it, there arises the possibility of adapting reaction not merely to the location of a single stimulus, but to the relative location of several stimuli. Responses may thus be adjusted not only to the direction of an object but to its form. On the basis of such adjustments a whole new field of possible discriminations is opened up.

The commonest arrangement for the production of a visual image is the double convex lens, which collects the rays of light diverging in their reflection from an object and brings them together again upon the sensitive retina. The lenses found in many simple invertebrate eyes seem, however, very ill adapted to the image-producing function. It is probable that they serve rather to intensify the effect of the light rays by bringing them together, than to give a clear-cut image (523). In the eye of certain invertebrates, such as the Nautilus, a cephalopod mollusk, while there is no lens, the opening admitting the light rays is so small that an inverted image might be formed through it, such as may be obtained through a pinhole. It is unlikely, however, that this eye is really an image-producing organ. Hesse includes under image-forming eyes only the camera or convex-lens eye, the mosaic eye, and the superposition eye. The last is a peculiar form of com-

pound eye where light can pass from one section to another, and where the image is formed by the coöperation of various refracting bodies (324).

The simplest and vaguest conceivable visual image would be that of a visual field whose different parts should differ in brightness.

An eye capable of furnishing indications merely of the direction from which the greatest illumination comes might produce this kind of an image, which would of course not allow the perception of objects, only that of bright-

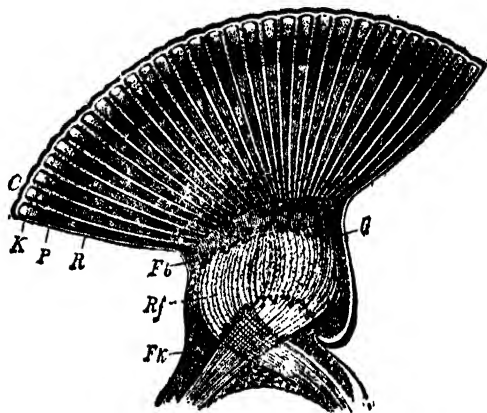


FIG. 11. — Diagrammatic representation of the compound eye of a dragon-fly. C, cornea; K, crystalline cone; P, pigment; R, nerve rods of retina; Fb, layer of fibres; G, layer of ganglion cells; Rf, retinal fibres; Fk, crossing of fibres. After Claus.

ness distribution. The compound eye found in crustaceans and insects would seem to be adapted chiefly for the perception of light direction and of moving stimuli. It consists essentially of a number of simple eyes so crowded together as to produce a common faceted cornea, each facet belonging to an eye. These facets are lens shaped, and back of each lies a refractile crystalline cone. Behind these, in turn, are nervous structures, the rods or retinulae, each separated from its neighbors by a pigment sheath. Light rays passing through each corneal facet probably produce a single spot of light on the retinula, and the

total image may thus be a mosaic formed of these spots (Fig. 11).

We have already seen that the orientations of certain animals to light seem to be produced through a tendency to take such a position that the two eyes shall be equally illuminated. If the two visual fields are combined in the case of such animals, as they are in our own binocular vision, under ordinary conditions the oriented position would give a field whose brightness is uniform throughout, while any other position would give greater brightness at one side of the field. If they are not combined, if there is no binocular vision, we cannot imagine what the resulting perception is. In the case of the starfish, we have an animal which seems to "see" a vertical white wall or dark wall that does not cast any actual shadow upon it; the starfish will direct its movements to or from such objects. Since the starfish has only eye-spots on the tips of its arms, with no arrangements for the formation of an image, and since the eye-spots are not arranged close enough together so that differences of illumination in different parts of a field could be represented by the different illumination of different eye-spots, we can explain the reaction to walls only, as Cowles (156) does, by supposing that those eye-spots and portions of the body nearest, say, a white wall, are more strongly illuminated than those furthest away. The response would then be one to different intensities of stimulation on different parts of the body, and these differences would not be seen as composing a visual field.

That the direction from which the light comes influences ants in finding their way is the opinion of Lubbock (441), Turner (722 a), and Santschi (654). The first named found that ants which had learned the way back to an artificial nest were confused when two candles which had stood

near the nest were moved to the opposite side. Turner made a similar observation, and Santschi suggests that the compound eye may perceive the direction of light by acting as a kind of sundial. He was able to make ants reverse their course when he altered the light direction by the use of mirrors.

§ 65. *Methods of Investigating the Visual Image*

Various methods of solving the problem as to the nature and accuracy of an animal's visual images have been used. One method consists in a study of the sense-organ itself, removed from the body. For example, Petrunkevitch (575) has thus investigated the sense of sight in spiders. These animals do not have the compound eye, but a number of simple eyes placed in groups. By a careful measurement of the possible minimal angles of vision in two spiders, *Phidippus* and *Lycosa*, the conclusion is reached that while a creeping insect about one square centimeter in size would be to the human eye so clearly visible at a distance of three metres that its species could be recognized, it would be only an indefinite moving speck to the eye of *Phidippus* and wholly beyond the range of vision of *Lycosa*.

Again, inferences are drawn as to the visual powers of animals from miscellaneous peculiarities of behavior. Thus Petrunkevitch (576) reports that a male spider of the species *Dysdera crocata*, in the courting stage, "watched" the movements of the end of a hatpin with which the observer was breaking clumps of earth, and when the movement ceased the spider approached the spot and scratched it with his front legs. The sight of a female spider digging had the same effect upon him, so evidently the visual

image which he received was hardly more definite than one of general size and movement. Bauer (28) reports of the mollusk *Pecten*, which has eyes of peculiar and complicated structure, that when a small quickly moving shadow is cast upon it, the tentacles are quickly withdrawn; large or slowly moving shadows have no effect, but a small, slowly moving shadow makes the animal stretch its tentacles and eyes towards the shadow. In this way, Bauer thinks, it is enabled to ascertain the nearness of its worst enemy, a starfish: apparently he supposes that the movement of the eyes towards the shadow gives an opportunity for visual perception of its form or characteristic movements. Wenrich (777) has recently obtained the following evidence of the formation of an image in *Pecten*. The bivalve normally responds only to a decrease in illumination, not to an increase. If a white card is moved across a black one, the card being not less than fifteen millimeters square and its distance not greater than thirty-five centimetres, *Pecten* responds by closing its shell, although the illumination is increased rather than diminished.

The chief lines of evidence, however, from which the nature of the visual image can be concluded are three: experiments on the visual perception of size, experiments on the visual perception of form, and experiments or observations on the recognition of visual landmarks in homing.

§ 66. *The Visual Perception of Size*

Bohn's observations on the mollusk *Littorina* show that its reactions are influenced by the size of the illuminated or darkened surface, as well as by the intensity of the light. When neither very wet nor very dry, *Littorina* will react to small objects in its neighborhood, whereas in an extreme

state of "hydratation" or desiccation it responds to the attraction or repulsion of the larger screens with fatal uniformity (80).

Plateau attempted to test the responses of certain Diptera to the size of an opening admitting light, by placing them in a dark room, into which light entered from two sources. One was a single orifice large enough to let the insects out; the other was covered with a net whose meshes were too fine to allow them to pass. The amount of light from the two sources could be made equal. When this was done, the insects, which were positively phototropic, sought the two equally often; if the light from either was made more intense, they went to that one. Plateau concluded both that the flies could not see the netting and that the area of the light source did not affect them (592). On the other hand, Parker found that the mourning-cloak butterfly did discriminate areas, flying to the larger of two sources of equally intense light (537).

This method of testing the image-forming power of an animal's eyes has been elaborated by L. J. Cole. He subjected animals with decided positive or negative phototropism to the influence of two lights made equally intense but differing in area, one coming through a piece of ground glass 41 cm. square, the other a mere point. Eyeless animals, the earthworm, for example, reacted equally often to each light. Animals whose eyes from their structure have been judged capable of perceiving merely the direction of light rays, such as the planarian *Bipalium*, confirmed the argument from structure by showing little more discrimination than the eyeless ones. On the other hand, animals with well-developed compound or camera eyes, for example certain insects and frogs, did distinguish between the lights, going, if positively phototropic, toward

the one of larger area ; if negatively phototropic, away from it (132).

Turtles showed a remarkable keenness of discrimination in the study made by Casteel (119), in which they were offered the choice of two compartments faced with cardboard carrying black lines on a white ground. Two turtles learned to discriminate between vertical lines eight millimeters in width and vertical lines two millimeters in width, and one gifted animal learned to distinguish, first, lines eight millimeters wide from lines one millimeter wide, then between a width of four millimeters and a width of one millimeter, then between four and two, and finally between three and two millimeters. Chicks proved equal to a discrimination between a standard circle six centimeters in diameter and one from one-fourth to one-sixth larger. The relative brightness of the circles was varied so that the chicks could not use this as a basis for their choices (102). White rats can discriminate circles thirty millimeters in diameter from circles fifty millimeters in diameter, and squares twelve centimeters a side from squares one centimeter a side (411). Discrimination of boxes differing in size but alike in form, placed in a row along a board, food having been put in one, was imperfectly learned by two *Macacus* monkeys; the errors leaned in the direction of taking the larger vessel (401). Raccoons were taught to distinguish perfectly between two cards, one $6\frac{1}{2} \times 6\frac{1}{2}$ inches square and the other $4\frac{1}{2} \times 4\frac{1}{2}$, shown successively. The animals were to climb on a box for food when the larger card was shown and to stay down when the smaller one appeared. As we shall see later, L. W. Cole, the experimenter, thinks the learning gave evidence not only of a spatial image, but of a memory image (134).

One apparent effect of size upon visual perception relates

to the distance at which an object produces a reaction. Caterpillars, for example, are described as giving evidence of seeing a slender rod extended toward them at a distance of about a centimeter; large masses they reacted to at somewhat greater distance (597). It is highly doubtful whether this means that the simple eye of the caterpillar could give a perception of two objects as differing in size if they were equally distant. Myriapods, which make very little use of sight and do not perceive their prey until they touch it, give evidence of seeing an obstacle having a rather broad surface, the size of a visiting card, at a distance of about 10 cm., if it is white and reflects much light, or if it is blue; but not if it is red.

§ 67. *The Visual Perception of Form*

The second method of studying visual images tests an animal's power to discriminate *forms*. Bumblebees were thought by Forel to evince a capacity to distinguish a blue circle from a blue strip of paper when they had previously found honey on a blue circle, even though the two had been made to exchange places. They flew first to the place where the blue circle had been, but did not alight upon the strip. Wasps also, according to Forel, distinguished among a disk, a cross, and a band of white paper, going first to the form on which they had last found honey (231). Turner (726) reports the ability of the honeybee to distinguish, in the open air, among "artefacts" of various forms (disks, cornucopias, and boxes), covered with various patterns such as transverse and longitudinal stripes, mottled surfaces, and spotted surfaces; if the bee had found honey in an artefact of a certain pattern it would select that pattern from among other patterns or

plain colors. Von Frisch (247) finds that bees can discriminate patterns like those of flowers, but fail with those very unlike flower patterns. This evidence, taken at its face value, indicates that the compound eye is able to furnish a fairly clear image, and not merely discriminations of light direction and movement.

Among vertebrates, various species of birds were experimented on by the method of placing cards carrying simple designs over glasses covered with gray paper, food being found always under the same card. The English sparrow and the cowbird both learned to distinguish a card bearing three horizontal bars and one bearing a black diamond from each other and from plain gray cards. On the other hand, the sparrow, curiously enough, did not succeed in discriminating vessels of different form; the cowbird was not fully tested with these, but gave some evidence of learning (610, 611). Pigeons were only moderately successful in a similar test (647). Breed (101, 102) and Bingham (56) investigated the form discriminations of the chick, using the more accurate method of offering a choice between compartments illuminated through openings of different forms. One out of three of Breed's chicks succeeded in discriminating between a circle and a square: Bingham's chicks distinguished between a circle and a triangle when the apex of the triangle was on top, but the discrimination broke down when the triangle had its base uppermost. The most careful work that has been done on the discrimination of forms or patterns by animals, up to the date of publication of this book, is that of Johnson (386). His apparatus allowed the presentation of two illuminated fields whose intensity could be perfectly controlled, with black bands across them whose width could be varied at will. He proposed four problems: (1) the width of stripes

necessary to make a striped field just distinguishable from a uniform field; (2) the just noticeable difference between the width of stripes on two fields; (3) the just noticeable difference in the direction of the stripes on two fields; (4) the just noticeable difference in brightness between two fields, one of which has stripes of equal brightness, while the stripes on the other are of unequal brightness. The chick's ability to distinguish a striped from a plain field proved to be about one-fourth that of a monkey or human being; when the problem of distinguishing between striped fields whose stripes were of different widths was presented, the monkey did ten times as well as the chick. For differences in the direction of stripes, the threshold of the chick was between twenty-five and thirty degrees; the monkey's was between two and five degrees: moreover, the monkey learned the discrimination in twenty trials, while the chick required 585. It seems practically certain that the chick is not a fair representative of the bird family as regards the clearness of its vision for form and size; the eye of a hawk is a proverb for keenness, and the ability of birds to find their food by vision demonstrates the high development of their eyes in image-forming power.

Among mammals, many dogs have been taught to distinguish printed letters on cards; Sir John Lubbock's poodle "Van" is a familiar example. Van learned to pick out cards marked "Food," "Bone," "Out," "Water," and the like, and to present each on its appropriate occasion. It took him ten days to begin to make the first step of distinguishing between a printed card and a plain one; in a month this was perfected and in twelve more days, when he wanted food or tea, he brought the right card one hundred and eleven times and the wrong one twice. The second mistake consisted in bringing the word "Door" instead of

"Food," which was taken as indicating that he really was paying attention to the look of the words (444). Such observations, however, are very inconclusive when compared with modern experimental studies where all the sources of error, from smell, for example, are carefully controlled. In Johnson's (386) study of the visual acuity of the dog, while two chickens and a monkey learned to distinguish a striped from a plain field in from three hundred to four hundred trials, dogs failed to learn in over a thousand trials, although the stripes were made nearly six times as wide. The dog could not distinguish between two visual fields unless they differed in intensity. Thus his visual images would seem to be far from clear. The eye of the dog, it may be noted, does not possess a fovea. Johnson thinks the dog's vision is useful chiefly for the perception of moving objects. Szymanski (702) finds that when dogs and cats have been trained to go to a box in a certain corner to get food, and the box is moved, the dogs show their lack of dependence on vision by displaying little tendency, as compared with the cats, to use this sense in finding the new situation of the box. Orbeli, however, obtained evidence by Pawlow's method that dogs could appreciate form and size differences (532 a).

The dancing mouse could not learn to distinguish two equal illuminated areas of different forms (820). Raccoons learned to discriminate a round card from a square one (134). Thorndike taught the two Cebus monkeys under his observation to come down to the bottom of the cage for food when a card bearing the word "Yes" printed on it was exposed, and to stay up when one bearing the letter "N" was shown. The conditions seem to have been complicated, however, by the fact that the two cards were not placed in quite the same position. Further

tests with cards carrying various designs showed varying degrees of capacity to distinguish them on the part of the monkeys (708). Kinnaman got negative results with his two *Macacus* monkeys in attempting to train them to distinguish cards such as those used in the later experiments of Porter on birds. His monkeys, however, proved able to distinguish vessels of different forms, "a wide-mouthed bottle, a small cylindrical glass, an elliptical tin box, a triangular paper box, a rectangular paper box, and a tall cylindrical can." These vessels differed in size as well as in form (401). Johnson's far more accurate experiments with the striped fields give the monkey a visual acuity about equal to that of man.

The question has been raised as to just what is meant by the term "form" in connection with the visual perceptions of an animal. When Bingham (56, 57) found that a chick failed to recognize a triangle whose base instead of its apex was uppermost, he suggested that the chick's previous discrimination of the triangle from a circle was not a discrimination of form in the true sense of the word, but based "on the unequal stimulation of different parts of the retina." Hunter (352) thinks that the animal in such a case is really discriminating *pattern* rather than form, and by pattern he means the whole design presented by the lighted forms and their surroundings. That is, a square lighted area inside a round tunnel would present to the animal a different pattern from a square lighted area inside a square tunnel; an animal might fail to recognize that the forms of the squares were identical when they were presented as parts of such different patterns. The writer of this book suggested in a review of Bingham's work¹ that his chicks, in failing to recognize that a triangle

¹ Psych. Bull., vol. 10 (1913), p. 320.

with apex down is the same form as a triangle with apex up, were demonstrating not their deficiency in form vision, but their lack of an abstract idea of triangularity. It may well be that such a perception of form in the abstract, such an ability to analyze forms out of patterns, depends upon the association between visual impressions and movements like the hand movements of a human being; few lower animals, of course, have the same kind of motor experience of objects that man possesses.

Special evidence of the comparative development of the visual image in different genera of ants is suggested by Wasmann to be furnished by the facts of mimicry. Certain insects belonging to orders other than the Hymenoptera inhabit ants' nests, and have in many cases become more or less modified to resemble their hosts. Wasmann thinks that these resemblances, which have been established on account of their protective value, are in insects living among ants of well-developed visual powers, such as would deceive especially the sense of sight, while in the "guests" of ants whose vision is poor, the mimicry is adapted to produce tactile illusions (762).

§ 68. *The Homing of Animals as Evidence of Image Vision*

The ability to find their way back to their dwelling place, or to any other locality that has a vital significance for them, is a power widely distributed among the most various forms of animals. We have considered, in the chapter on the Chemical Sense, the part which smell plays in this process, and on page 100 we noted the fact that the perception of light direction is not wholly without influence in some cases. The common human method of path-finding is by the recognition of visual landmarks: when we

set out from a familiar region into a strange region, we fix our attention on the appearance of the surroundings at critical points and turnings, and on the homeward journey guide ourselves by identifying these points through vision. Where it can be shown that animals are influenced in their homing journeys by the appearance of the surroundings, we have evidence that their vision must involve some perception of the form and detail of objects. The fiddler crab "remembers" the location of its nest, but just what the memory depends upon is not clear. On one occasion the observer, Pearse (568), covered the nest with his foot; the female crab to which it belonged waited fifteen minutes until he moved his foot, and then dashed for the nest and tried to reopen it. Lubbock's (441) demonstration that ants do not use visual landmarks on frequented roads will be recalled (see page 97).

In the case of bees, on the other hand, there is a good deal of evidence in favor of the use of visual landmarks in homing. It is true that Bethe (51) was unable to note any disturbance in the flight of bees back to the hive when he altered the appearance of the hive, or when a large tree that stood near the hive was cut down. But in this case the bees had thoroughly learned the location of the hive and had probably ceased to need landmarks in its immediate environs. Lubbock found that bees from a hive near the seashore, when taken out on the water and liberated, were unable to find their way home, although the distance was less than their usual range of flight on land; and he ascribes their failure to the lack of visual landmarks to guide them (441). Bethe, who thinks bees are guided home neither by vision nor by smell, but by an unknown force to which they respond reflexly, also liberated some bees at sea about 1700-2000 metres from their hive, which was

near the foot of Vesuvius and beside some very tall and conspicuous trees. The bees failed to return, and Bethe thinks, if they were guided by vision, the mountain and the trees should have aided them to do so (53). It may well be, of course, that bees cannot see objects at such a distance. Besides his observation that changing the appearance of a hive did not disturb the bees in their homing flight, Bethe urges against the visual memory hypothesis an observation on a hive which had on one side of it a garden, and on the other side a town, which he thinks the bees never visited, as food was to be had in abundance in the garden. Yet when liberated in the town they flew back to the hive with an accuracy certainly not born of their acquaintance with the locality (51). Von Buttel-Reepen, however, doubts whether the bees really never visited the town. Bethe's most striking illustration of his unknown force, however, is derived from his "box-experiments." If a number of bees are carried in a box some distance from the hive, on being liberated they fly straight up in the air. Some of them will return to the hive, but if the distance is great enough, many will drop back upon the box. Now if the box has moved only a few centimeters away during the flight of the bees, they will drop back to the precise spot where it was, and take no notice of its new location. If they were guided by vision, Bethe urges, they could easily see the box (51, 53). This, says von Buttel-Reepen, is arguing that their visual memory must be like ours if it exists at all; it may be a memory, not of the appearance of the box, but of its locality. He himself, repeating Bethe's experiments, observed the bees on dropping back after their upward flight, hunting not at the place where the box had been, but at a height which was about that of their home hive entrance. He thinks that an important

feature of the bee's visual memory consists in a power of accurately estimating height above the ground. If the entrance to the hive be raised or lowered 30 cm., all the returning bees will go to the old place, and it will be hours and sometimes days before they find the new one. Moreover, the same bees tend to return to the same corner of the opening each time. When a row of hives had been arranged, some with openings in front and others with openings at the side, bees which had been driven home in haste by a storm would sometimes try to enter the wrong hive, but if their home hive opened on the side, they would attempt to enter the foreign hive on the corresponding side (115).

Turner (723 a) reports that the burrowing bees (*Anthophoridæ*) use visual landmarks to identify the location of their nests, and are disturbed if the landmarks are altered.

In the solitary wasps, although Fabre is inclined to assume a "special faculty" of homing, independent of visual memory, basing his assumption on experiments where the wasps returned to their nests, from which they had been transported in a box to a distance of three kilometers (218, Series I); yet the evidence obtained by the Peckhams seems fairly conclusive in favor of memory for visual landmarks. The solitary wasps have been shown, by the observations of the Peckhams to depend upon sight for the return to the nest (572, 573), and the same conclusion is indicated for the social wasps by Enteman (206). The Peckhams' belief in the visual memory of solitary wasps rests first upon the fact that the wasp, upon completing her nest, always spends some time in circling about the locality, in and out among the plants, as if she were making a careful study of the region. On leaving the nest a second time she omits this process and flies straight away. A

similar "locality survey" is made by hive bees and by social wasps. Secondly, the Peckhams argue that if the wasp does not remember her nest by landmarks, it ought to make no difference to her when the surroundings are altered in any way. They found, however, that a wasp of one species could not discover her nest when a leaf that covered it was broken off, but found it again without trouble when the leaf was replaced. Another wasp abandoned the nest she had made for herself with much labor, because the Peckhams, to identify the spot themselves, drew radiating lines from it in the dust. A third argument against the existence of a special sense of direction is the fact that wasps sometimes are unable to find their nests. In one case the Peckhams dug up the nest of a wasp and she made another five inches away. After an absence of three hours the wasp returned, and seemed to be puzzled as to whether the old spot or the new one were the place of her nest. "At first she alighted upon the first site and scratched away a little earth, and then explored several other places, working about for twelve minutes, when she at last found the right spot." Similarly, when a wasp that was carrying her prey left it for a few moments to go to the nest, as many of them do, apparently to see that all is right there, if any of the surrounding objects were altered she often had great difficulty in finding the prey again. On one occasion a wasp of another species dug its nest in the midst of a group of nests of the *Bembex* wasp. These latter are usually dug in a wide bare space of earth which has no vegetable growth to serve as a landmark. When the intruder had finished her nest, it looked just like the *Bembex* holes. She went away, secured a spider, and when she returned she could not find her nest. "She flew, she ran, she scurried here and there, but she had utterly

lost track of it. She approached it several times, but there are no landmarks on the B. field. After five minutes our wasp flew back to look at her spider," which she had dropped about three feet away, "and then returned to her search. She now began to run into the B. holes, but soon came out again, even when not chased out by the proprietor. Suddenly it seemed to strike her that this was going to be a prolonged affair, and that her treasure was exposed to danger, and hurrying back she dragged it into the grass at the edge of the field, where it was hidden. Again she resumed the hunt, flying wildly now all over the field, running into wrong holes and even kicking out earth as though she thought of appropriating them, but soon passing on. Once more she became anxious about the spider, and, carrying it up on to a plant, suspended it there. Now she seemed determined to take possession of every hole that she went into, digging quite persistently in each, but then giving it up. One in particular that was close by the spider seemed to attract her, and she worked at it so long that we thought she had adopted it, for it seemed to be unoccupied. At last, however, she made up her mind that all further search was hopeless, and that she had better begin *de novo*; and forty minutes from the time that we saw her first she started a new nest close to the spider, as though she would run no more risks" (572). An occurrence of this kind certainly lends color to the 'recognition of landmarks' theory. On the other hand, the *Bembex* wasps themselves find their nests with unerring accuracy, though there is no landmark in the field. Fabre noted that *Bembex* wasps could not be led astray by any modification of either the look or the smell of their nests, and thought a peculiar form of space memory, unparalleled in our own experience, must be involved in the nest-find-

ing of this species (216, Series I, 263). Bouvier, repeating Fabre's experiments on *Bembex*, obtained a different result. When a stone, for example, that had been at the mouth of a *Bembex* nest was moved a distance of 2 dm., the wasp, returning, went to the stone. Bouvier accordingly maintains the visual landmark hypothesis (99). Ferton holds the same view with regard to a species of wasp that makes its nest in shells. If during successive absences on the wasp's part the shell is moved from position A to position B, and later from B to C and from C to D, the wasp, returning, goes in turn to each of the positions that the shell has occupied. "In time, she omits to go to A, then to B. Little by little, the image of the previous locations of her nest is effaced in the insect's memory." When she has found it, after each displacement, she makes a new "locality survey," before starting off again (217).

Turner (728) reports that the mason wasp is certainly guided by visual landmarks. A wasp had built her nest on a window casing. The window was one of four in a row; the shades on the other three were down. When the shade on the window where the wasp's nest was situated was drawn down and that of the next window drawn up, the wasp returning sought her nest on the casing of the next window, which was now the only light one in the row.

Solitary wasps and bees, which need to find their way back, not to a nest whose position remains fixed, as is the case with ants and honey bees, but to nests in new positions from day to day, almost certainly have to depend upon their recognition of visual landmarks, and hence we have another evidence that the compound eye can give a serviceable image.

The migration of birds is still an unsolved problem.

That carrier pigeons depend on visual landmarks is maintained by many authorities. They do not fly at night, nor do they home well in cloudy weather. Young pigeons have to be trained on short distance flights, though of course this might be the case if they depended on some other power than recognition of visual landmarks. Migrating birds in some cases fly long distances over the ocean, where no visual clues can be furnished. Watson (769) caused some noddy and sooty terns to be carried in a steamer from the Tortugas Islands to the latitude of Cape Hatteras, a distance of nearly a thousand miles, where they were liberated. The locality is far out of their range of habitat, yet they returned to their breeding place in about a week. Hachet-Souplet¹ suggests that a very vague visual image, of objects too far off to be clearly seen, may be used in such long distance homing, but the curvature of the earth would interfere with a bird's getting even a vague image of any surroundings that could be familiar to it.

§ 69. *Class V: Reactions adapted to the Distance of Objects*

The factors that make possible the perception of the third dimension, depth, or distance outward from the body, in invertebrate animals are little known. Certain invertebrates do give evidence of the power to judge distance. The hunting spiders, for example, which do not make webs, but pursue their prey in the open, leap on it from a distance of several inches. Dahl thinks their distinct vision is limited to two centimeters (168), and Plateau says capture is not attempted until the prey is within this distance (596). The Peckhams, however, tested a hunting spider by putting

¹ VI Congrès Int. de Psychologie, 1909, p. 663. I have been unable to obtain the original article.

it at one end of a narrow glass case sixteen inches long, at the other end of which a grasshopper was placed. When eight inches from its victim, the spider's movements changed, and at four inches the leap was made¹ (571).

Reactions of this character, where the animal makes a single movement adapted to the distance of an object from it, are almost the sole evidence we can get of accurate perception of the third dimension. The alleged performance of the jaculator fish, which, as described by Romanes, "shoots its prey by means of a drop of water projected from the mouth with considerable force and unerring aim," the prey being "some small object, such as a fly, at rest above the surface of the water, so that when suddenly hit it falls into the water," would involve distance perception (640, p. 248). The catching of insects on the wing by various amphibians, reptiles, and birds has the same significance. A salamander cautiously stalking a small fly will not strike until it gets within a certain distance. In *Necturus* and in other animals the pause just before snapping at food has been suggested to be for the purpose of proper fixation (785).

Training an animal to jump from one support to another is a method that has been used to study distance perception in the mouse (775) and white rat (634). Waugh put a mouse on a disk and raised it a certain distance above a support; he then measured the time the mouse hesitated before jumping, when the height of the disk was varied. From the fact that the mice hesitated longer, the greater the height, he inferred some visual perception of distance.

¹ Porter observed that the distance at which spiders of the genera *Argiope* and *Epeira* could apparently see objects was increased six or eight times if the spider was previously disturbed by shaking her web (612). This, of course, does not refer to the power to *judge* distance.

When, however, the mice were required to judge which of two partitions was nearer to their starting-point, and to turn to the right or the left in accordance with this preliminary judgment in returning to their nest, they failed: this really involves a rather complex type of learning, and is a much less fair test of the mere ability to perceive distance than is the instinctive reaction of jumping. In Richardson's (634) study of the rat, the animals were trained to jump from one horizontal support to another. They proved able to judge quite accurately the direction of the platform to which they had to jump, but when its distance was altered they could not adapt themselves, and jumped either too far or too short.

Yerkes's tests of the so-called 'sense of support' in tortoises indicate, like Waugh's experiments on the mouse, some power of estimating distance by vision in these animals. He experimented, it will be remembered, with individuals belonging to three classes: land-dwelling, water-dwelling, and amphibious. The first mentioned would crawl off the edge of a board 30 centimeters above a net of black cloth only with much reluctance when their eyes were uncovered; when blindfolded they would not move at all. The water tortoises plunged off without hesitation from a height of 30 centimeters, but hesitated slightly at 90 centimeters, although some individuals would take the plunge at once even from a height of 180 centimeters. When blindfolded, all of the water tortoises rushed off at any height. The land-and-water-dwelling tortoises hesitated at 30 centimeters and at 90 centimeters showed a conflict of impulses, trying to catch themselves before launching off. When blindfolded they would not leave the board at all, though they moved about upon it freely (810).

Some of the most important conditions of distance perception in our own experience are lacking in the lower vertebrates and in invertebrates. Stereoscopic vision, the appearance of solidity given to objects by the fact that the visual fields of the two eyes combine, thus producing blending of two slightly different views of the object looked at, has been held to be dependent on the partial crossing of the optic nerves on their way to the brain, whereby each retina sends nerve fibres to both hemispheres of the brain. This arrangement does not appear in the animal kingdom below the birds; whatever function it plays in space perception is, then, absent from reptiles, amphibians, fish, and invertebrates. Certainly stereoscopic vision cannot exist in animals whose eyes are so placed that the same object cannot be seen by both, as is the case with most fishes. In birds whose eyes are situated too far toward the sides of the head for the same object to cast its images on the foveas or centres of the two retinas, there appears to be a secondary fovea in each eye, so placed as to suggest that it serves binocular vision, while the primary fovea is used for monocular vision. In certain mammals the eyes are placed so far towards the sides of the head that the binocular field is very small. This is probably the reason why rodents do not have a more accurate perception of distance. The writer made some simple tests on the use of binocular and monocular vision by the rabbit (756). When the animal was sitting quietly, two bits of food of equal size and kind were held at equal distances from the rabbit's nose, one straight in front, the other directly to the right or left of the rabbit's head. In forty-eight out of fifty trials, the rabbit turned towards and secured the food at the side rather than that in front, thus showing its dependence on monocular rather than binocular vision.

Convergence, the turning of the eyes toward each other to bring the two images of an object on the central part of the retinas, which is an important aid to human estimations of distance, is also necessarily lacking in animals without binocular vision. A third factor in our own perceptions of distance, the accommodation of the crystalline lens, that is, the alteration of its convexity through the pull of the accommodation muscle to enable it to focus objects at different distances, has been carefully studied in connection with the lower animals by Beer. Through experiments on the refractive powers of eyes dissected from the dead animal, he reached the conclusion that no invertebrates but cephalopods have the power of accommodation. It is rudimentary or lacking also in some members of the fish, lizard, crocodile, snake, and mammal families. In cephalopods, fishes, amphibians, and most reptiles, the process of accommodation does not involve a change in the form of the lens, but an alteration in the distance between the lens and the retina. The device of increasing the curvature of the lens for vision of near objects appears first in certain snakes, and is found throughout the higher vertebrates (33, 34, 35, 37).

Where accommodation does not exist, as in most invertebrates, it is possible to trace other arrangements for adapting vision to the distance of the object seen. Thus in compound eyes, part of the eye may be adapted to near vision and part to far vision. This is suggested by the fact that some of the little tubes, or ommatidia, of which the compound eye is composed, diverge from each other by a less angle than others, indicating that they are suited to the reception of more nearly parallel rays. In insects with both simple and compound eyes one form may be used for near and one for far vision. It has been main-

tained (182) that the simple eyes function with the compound eyes to respond to changes in the depth of objects, since such changes would alter the angle at which light rays from the object would fall on the two sets of eyes. Spiders appear to have the principal eyes adapted for far vision and the auxiliary eyes for near vision, while one spider, *Epeira*, has part of the hinder median eye adapted to each (324).

§ 70. *Some Theoretical Considerations*

The temptation is strong to speculate upon the essential nature of the conditions which make possible true space perception, the simultaneous experiencing of sensations that are referred to different points in space. Such speculation must be of the most tentative description, yet the following suggestions seem not wholly unwarranted by the facts. For one thing, it looks probable that the ability to suspend immediate reaction is essential to space perception. Can a spatial complex of sensations occur in the experience of an organism unless that organism is capable of receiving a number of stimuli on a sensitive surface and of suspending, for a brief period at least, all reaction? Let us take as an example of such a complex a visual field, within which different color and brightness qualities are arranged in definite order, some above, some below, some to the right, others to the left. Could such a balance of tendencies to move the eye as is involved in the simultaneous perception of a number of elements preserving regular space relations to each other have been brought about unless no single one of the tendencies were irresistible? One can readily imagine an eye functioning in such a way that every stimulation of it, though occa-

sioned by rays from several different directions acting simultaneously, should issue at once in a resultant movement. Would not the accompanying consciousness be a single resultant sensation, rather than a complex of spatially ordered elements? It is a good deal easier, of course, to ask than to answer such questions.

Again, the power of getting true spatial images seems to be bound up closely with the power of moving the sensitive surface. We get our best tactile space perceptions through active touch, involving movement of the hands and fingers; our visual space perceptions are profoundly influenced by eye movements. Where the movements of an animal's body as a whole are very rapid, as in the case of winged insects, this fact may compensate for the immovability of its eyes. Forel, as we have seen, thinks that insects which can explore objects by moving the antennæ, bearing the organs of smell, over them, may have smell space perceptions, such as are unknown to our experience; they may perceive the shape and size of odorous patches as we could do if our organs of smell were on our hands (233). Now, movement of a sense organ brings about the same result that movement of a stimulus across a resting sense organ does; that is, the stimulus affects different points of the sensitive surface in succession. But the vital significance of the two is quite different; movement of an object across a resting sense organ means very likely that the object is alive; it must be instantly reacted to, and the speed of the reaction is unfavorable to the formation of a true space perception. Movement of the sense organ, however, gives a series of impressions on successive points of the sensitive surface, from a resting object. While the sense organ is being moved, it is probable that other reactions of the animal will be suspended. Whether any part in the forma-

tion of that complex conscious content which we call a spatial image, consisting of different sensations simultaneously apprehended, is played by the "lasting over" of the impressions on one sensitive point after the stimulus has passed on to the next, a phenomenon which we find both in touch and in sight sensations, it is impossible to say. We are, however, apparently justified in the statements that the essence of space perception, as distinct from other conscious processes that may accompany spatially determined reactions, is the presence of an image in the sense above defined, and that a movable sense organ is an important condition for the production of such an image.

CHAPTER X

THE MODIFICATION OF CONSCIOUS PROCESSES BY INDIVIDUAL EXPERIENCE

THE reactions of animals to stimulation show, as we review the various animal forms from the lowest to the highest, increasing adaptation to the qualitative differences and to the spatial characteristics of the stimuli acting upon them. It is therefore possible to suppose that the animal mind shows increasing variety in its sensation contents, and increasing complexity in its spatial perceptions. But besides this advance in the methods of responding to present stimulation, the higher animals show in a growing degree the influence of past stimulation. While a low animal may apparently react to each stimulus as if no other had affected it in the past, one somewhat higher may have its reaction modified by the stimulation which it has just received. An animal still more highly developed may give evidence of being affected by stimuli whose action occurred some time before; and finally, in certain of the vertebrates, perhaps, as in man, conduct may be determined by the presence in consciousness of a memory idea representing a past stimulus. "Learning by experience," or "associative memory," as we saw in Chapter II, has been regarded as the evidence *par excellence* of the existence of mind in an animal. That it does not serve this purpose to entire satisfaction was also pointed out in that earlier chapter, and will be more clearly apparent as we survey

in the following pages the various ways in which an organism's past experience may modify its behavior. For each type of modification we shall try to find a parallel in human experience, and thus to interpret, so far as possible, the conscious aspect of the learning process. To begin with, we shall distinguish between those modifications which depend on some comparatively lasting alteration in the organism (in its nervous system if it has one), that is, the kind of modification which is ordinarily understood by the term "learning"; and modifications which are due to a change essentially temporary in its character, in the physiological state of the organism. Even in the lowest animals the effect of a stimulus depends on the organism's physiological condition, and this condition is often the result of stimulation recently received.

§ 71. *Modifications Due to Essentially Temporary Physiological States: (a) Heightened Reaction as the Result of Previous Stimulation.*

Sometimes the effect of the stimuli which the organism has just received increases the violence of its response to a given stimulus. Thus in the earthworm Jennings points out that various stages of excitability may exist, due to the action of previous stimulation, and varying all the way from a state of rest, where a slight stimulus produces no effect, to a condition of violent excitement, where moderate stimulation will cause the animal to "whip around" into a reversed position or wave its head frantically in the air (377). This increased excitability suggests the "nervous irritation" produced in a human being by an accumulation of disagreeable stimuli; an increased feeling of unpleasantness accompanied by more diffused organic

and kinæsthetic sensations is its accompaniment in the human mind.

When the same stimulus is repeated, in many cases the effect of this heightened excitability is shown by the organism's performing in succession different forms of the negative reaction until one of them is successful in getting rid of the stimulus. The ciliate *Stentor* furnishes us with an example. When attached by its stem, if it is strongly stimulated, say, with a glass rod, several times in succession, it first tries its commonest negative reaction, bending over to one side. If the stimulus continues, it reverses momentarily the direction in which the cilia are whirling. If this, several times repeated, does not succeed in getting rid of the stimulus, the animal contracts strongly upon its stem. This also is continued for some time, but if the stimulus too is kept up, the *Stentor* finally breaks from its moorings and swims off (370).

There are many examples of similar behavior in other animals. *Hydra* in certain cases tries first the ordinary negative response of contraction, and later moves away from the region it has been occupying (751 a). Frandsen found that if the slug *Limax maximus* has a tentacle touched several times in succession, it at first withdraws the tentacle and turns away from the stimulus. Later, it may move toward and push against the stimulus, and do the same if the touch is on the side of its body, resisting and curving around the obstacle — another way, of course, of getting rid of it (236). Preyer, again, observed a very pretty instance of this sort of behavior in the starfish. He slipped a piece of rubber tubing over the middle part of one of the arms of a starfish belonging to a species in which those members are very slender, and found that the animal tried successively various devices to get rid of the foreign

body, to wit, the following: rubbing it off against the ground, shaking it off by holding the arm aloft and waving it pendulum-wise in the air, holding the tube against the ground with a neighboring arm and pulling the afflicted arm out, pressing other arms against the tube and pushing it off, and, finally, as a last resort, amputating the arm. This, says Preyer, is intelligence, for the emergency is not one normal to the animal, and it is adapting itself to new conditions (617). It would, however, be demanding too much even from intelligence to suppose that the starfish's behavior is entirely new. A human being, capable of ideas, could only, in a similar predicament, "think of," that is, call up, ideas of the behavior which on former occasions somewhat resembling the present had proved effective. Do such cases of the trial of different devices indicate that the animal concerned calls up any kind of idea or image of each device before putting it into practice? Decided evidence in favor of such a supposition might be furnished if the "trial and error" needed to be gone through with only once. A human being brought into such conditions and guiding his conduct by ideas would, if placed in a similar emergency soon afterwards, immediately recall the idea of the successful action and waste no time over the unsuccessful ones. But we have no reason to think that such is the fact with our primitive animals. Preyer's starfish, when confined by large flat-headed pins driven into the board on which it lay, close up in the angles between its arms, managed to escape by trying a large variety of movements, and gradually diminished, Preyer says, the number of useless movements made in successive experiments (617). O. C. Glaser, on the other hand, found that the echinoderm *Ophiura brevispina* does not improve at all with practice in removing obstructions from its

arms. The very versatility of the starfish, this writer thinks, tells against its perfecting any one movement through experience (260). Stentor and Hydra go through the same series of reactions each time, without apparently being influenced by their previous behavior. And again we must remind ourselves that there is no reason why their conduct, adaptively regarded, should be otherwise. An animal with so little power of distinguishing qualitative differences among stimuli cannot be in any way aware that the stimulus which affects it a second time is going, as in the previous case, to be so persistent that the ordinary negative reaction will not get rid of it. Further, each reaction of the series performed by the animal is more disturbing to its ordinary course of life than the preceding one. The Stentor can bend to one side and still continue the food-taking process; if it reverses its ciliary action, feeding must be momentarily interrupted; while contraction on the stem and breaking loose from its moorings are still more serious infractions of the normal routine. It would be decidedly disadvantageous to take the last step while there was any chance that milder measures might prevail.

In all probability, since the behavior just described has no permanent effect upon the animal, it is physiologically due, as Jennings suggests (375), to the overflow of the nervous energy set free by the stimulus into first one channel and then another. In most cases the movements resulting are all adapted to getting rid of the stimulus, though only one of them is successful in so doing; but we have on record one case where, in a supreme emergency, the stimulus being not only repeated but increased in intensity, every possible outlet is tried, whether it has any fitness to the situation or not. This was observed by Mast, testing the effect of increased temperature on the reactions of pla-

narians. The first influence of such increase from 23 degrees to 26 degrees C. is to produce heightened activity and positive reactions. Then, from 26 degrees to 38 degrees, the reactions are negative. From 38 degrees to 39 degrees, violent crawling movements set in, and then, curiously enough, the righting reaction is given, perfectly irrelevant, of course, to the conditions. Finally, the anterior and posterior ends are turned under, the central part is arched upward, and the animal falls over forward on its back (462).

In all these cases where repetition of the same stimulus produces successively different forms of the negative reaction increasing in violence, it is most natural to think of the psychic accompaniment as an increasing degree of unpleasantness. In our own experience, repeating a stimulus does not alter the quality of the resulting sensation, except where the structure of a special sense organ is a modifying factor, as in the case of visual after-images. A decidedly disagreeable stimulus acting repeatedly on a human being may produce unpleasantness that grows more and more intense until it is unbearable; the behavior of a human being under such circumstances is much like the animal behavior we have just been describing. Various movements calculated to get rid of the stimulus are tried, each more energetic than the last. Hence, if the lower animals behaving thus are conscious, we may plausibly assert that their consciousness under these circumstances is increasingly unpleasant. But the human experience in such a case would be, or might be, further characterized by the presence of ideas. That is, the human being would *think* of the different ways to get rid of the stimulus one after another. This many, at least, of the animals that try different negative reactions are apparently in-

capable of doing. We judge that they are so by the simple fact that on being subjected after an interval to the same presumably disagreeable stimulus, they do not at once make the reaction that was previously successful in getting rid of it. A human being, recalling that reaction in idea, would be able to do so. We shall see in the next chapter that many animals, while they do not learn the successful reaction from a single experience, do gradually diminish the number of unsuccessful ones made in a series of experiences. It is quite possible that this will prove to be true of all animals, as experimental evidence accumulates.

§ 72. *Modification Due to Essentially Temporary Physiological States: (b) Cessation of Reaction to a Repeated Slight Stimulus.*

The type of modified response just described occurs when the stimulus is strong, and presumably injurious. When it is of moderate intensity only, the organism tends to respond less and less violently as the stimulus is repeated at short intervals, until finally the response lapses entirely. The Ciliata *Vorticella* and *Stentor*, which spend a part of their time attached to solids by a contractile stem, contract at the first application of a moderately intense mechanical stimulus, but fail to react at all when the stimulus is several times repeated (370). *Hydra* responds to mechanical stimulation by contraction, but gets used to the process when repeated and gives no further reaction (751 a). The sea-anemone *Aiptasia* reacts by a sharp contraction to a drop of water falling on it; later it ceases its response to this stimulus. If exposed to light, it contracts and remains in this state for some hours, but afterwards expands again (374). The annelid *Bispira voluticornis*

was found by Hesse to give no further response to sudden shadows when the stimulus was frequently repeated (321). Hargitt (285) reports the same of tube-dwelling annelids. Von Uexküll reports that the sea-urchin *Centrostephanus longispinus* ceased to respond to shadows after three successive stimulations (736). Nagel observed that certain eyeless mollusks which react to sudden darkening very quickly get used to the stimulus and cease to respond; often after one reaction they decline to react for several hours.¹ The mollusks that responded to sudden brightening rather than to shadows, that were in Nagel's phrase photoptic rather than skioptic, took longer to become accustomed to repeated stimulation, but did so by gradually weakening their reaction (520). A web-making spider that was found by the Peckhams to drop from its web at the sound of a large tuning fork declined to disturb itself after the stimulus had been repeated from five to seven times (570). Ants "become used" to the ultra-violet rays which they ordinarily avoid (220). The responses of dragon fly nymphs to light are less marked as the stimulus is repeated (636), and the same is true of mosquito larvæ (338).

Where such an effect as this is temporary, the most obviously suggested cause for it is *fatigue*. In our own experience this word is used chiefly with reference to motor processes; we perceive a certain signal, but are too fatigued to respond. On the sensory side, when a repeated or continued stimulus is no longer perceived, we call the phenom-

¹ The opposite phenomenon is reported by Rawitz of the mollusk *Pecten*, whose response to a shadow was the shutting of its shell. Repeated or long-continued shadowing, instead of doing away with the reaction, caused the animal to remain with closed shell for a long time; an intensification of the reaction which suggests the effect of summation of stimuli (628). We may infer that the stimulus in such a case is injurious.

enon one of *adaptation*. In true sensory adaptation, the sense organ becomes incapable of responding to the stimulus; for example, a person who has been for some time subjected to a certain odor is unable to smell it any more, however much he tries. Closely related to this phenomenon and yet different from it, is the lapse of attention to a repeated stimulus: we no longer notice the ticking of a clock, although the sense organ is unaffected by its continuance, and we can quite well hear it if our attention is attracted in that direction.

That the failure of Stentor to respond to successive stimuli is not due to motor fatigue appears quite certain to Jennings, since under favorable conditions he has obtained reactions from the animal for a period far longer than that occupied by the process of getting used to slight mechanical stimulation (370). And in most of the cases cited, the acclimatizing process seems to occur too rapidly to make fatigue of the motor apparatus probable. In the lower animal forms, sensory adaptation offers the most natural explanation for the phenomenon; in the higher animals, lapse of attention is very likely also involved. The modification of consciousness in both cases would be the loss of the sensation; where adaptation occurs, the sensation would be for the time irrecoverably lost; where there is merely lapse of attention, it could be regained by a proper direction of attention.

A much discussed case of the cessation of response to a repeated stimulus is found in connection with the food-taking reaction. One would expect the dominant condition here to be loss of hunger, and as a matter of fact, observers of the feeding processes in many lower animals have found that such reactions cease or turn into negative responses when the animal is satiated; although Piéron

indeed reports that while the responses of *Actinia equina* and *A. rubra* to mechanical stimulation cease on repetition of the stimulus, those to food stimulation continue indefinitely (581). If the change from food-taking to negative reaction has a conscious accompaniment, this might naturally be thought of as a change from pleasant to unpleasant affective tone. Nagel observed that if a ball of filter paper soaked in fish juice were placed upon one of the tentacles of the sea-anemone *Adamsia*, it was seized as eagerly as a ball of fish meat, but that when this deception had been several times repeated, the ball was held for a shorter period each time, and was finally rejected as soon as offered. Nagel is inclined to think that this is learning by experience, and points out that the psychic life of *Adamsia* must possess little unity, for the "experience" of one tentacle does not lead other tentacles to reject the paper balls at once (521). Parker finds similar behavior in *Metridium*, and explains it by saying that the filter paper offers but a weak food stimulus, and that "the successive application of a very weak stimulus is accompanied by . . . a gradual decline in the effects, till finally the response fails entirely"; in other words, that we have adaptation to a food stimulus (533). Jennings fed *Aiptasia* alternately with pieces of crab meat and with filter paper soaked in meat juice, the result being that the fifth piece of filter paper was rejected — but so was the crab meat thereafter. Jennings came to the conclusion that the phenomenon is due simply to loss of hunger on the animal's part, and that where Parker found that the crab meat would be taken after the filter paper was refused, it was because the latter was a weaker stimulus and naturally was the first to call forth the effects of satiety. The objection to the hunger hypothesis is that other tentacles of the same animal will react after one

tentacle has stopped; satiety ought surely to affect the entire organism (374). Allabach, in the light of these researches, made a careful study of *Metridium*. She disposes of the psychic learning by experience theory of Nagel by saying that the only experience upon which the animal could reject the filter paper must be experience that it is not good for food. This could be learned only by swallowing it; but the failure of the reaction occurs just as well when the animal is prevented from swallowing the filter paper. That the phenomenon is not one of adaptation to weak stimuli is shown by the fact that it may be brought about by successive feedings with meat which is not allowed to be swallowed. It cannot be due to loss of hunger, for this is experimentally shown to affect all the tentacles at once. Allabach concludes that it is simply a case of local fatigue of the tentacles. The taking of food by a tentacle involves the production of a considerable quantity of mucus, the immediate supply of which is probably exhausted after a few reactions, and a short period of rest is required (3). Parker (551) is still of the opinion that adaptation is the proper explanation for the phenomenon.

Another case of the cessation of reaction to a repeated stimulus is reported by Wasmann of ants in an artificial nest, which assumed the fighting attitude in response to the movement of a finger outside the nest, but after two or three repetitions of the motion were no longer disturbed (762). Where animals as high in the scale as the ant and spider are concerned, it is possible that this process of getting used to a stimulus may involve rather a dulling of emotion than a disappearance of sensation. This phenomenon also is familiar in our experience, and may be called emotional adaptation.

That adaptation is itself adaptive hardly needs to be

emphasized. As Jennings suggests, if the sea-anemone that contracts at the first ray of light were to remain contracted in steady illumination, it would lose all chance of getting food under the new conditions (374). The negative reactions ordinarily involve interruption of the food-taking process, and it is important that they should not be continued in response to stimulation that is relatively permanent. Hargitt thinks that the loss of reaction to repeated shadows which he observed in marine worms may be an adaptation to the varying illumination caused by ripples at the surface of the water (285).

A very important psychological question concerns the permanence of the effects of adaptation. Sensory adaptation and lapse of attention to repeated or continuous stimuli, as these phenomena are met in our own experience, are not considered phenomena of learning at all. The former is purely temporary in its effects: the person who has become so used to an odor that he cannot smell it shows no effects of this experience half an hour later. The effect of familiarity on emotion and on attention is more lasting: one's loss of attention to a clock ticking in one's room may persist despite more or less prolonged absences from the room, although a sufficiently long absence, during which one encountered no ticking clocks, would cause the sound to be noticed again. The loss of emotional response to a familiar stimulus may persist for some time. Emotional adaptation and lapse of attention to continued stimuli may fairly be termed learning in proportion as their effects are more than temporary.

In many cases, the effects of adaptation on animal reactions last over a considerable interval between the stimuli. This seems to be increasingly the case, the higher the animal. Thus *Hydra*, which is only a cœlenterate, if it is allowed to

reach full expansion after having contracted at a touch, will respond to the second touch just as it did to the first; the stimuli, to exert any influence on later reactions, must come in quick succession. On the other hand, in the responses of mollusks to shadows, the experiences of one day appear to extend their effects to the following day (520, 588, 590). Here we are dealing with a new type of modification by experience, though one which develops directly out of sensory adaptation; namely, the relatively permanent dropping off of useless movements.

§ 73. *Modifications Due to Relatively Permanent Effects of Stimuli*

In true learning, the conscious experience and the behavior of an animal suffer changes so lasting, relatively speaking, that they cannot be set down as due merely to adaptation of the sense organ, muscular fatigue, hunger, satiety, or any other variable physiological state of the organism. On the other hand, as we saw in Chapter II, the modifications must occur rapidly enough so that there is not time for actual changes in the animal's muscular structure to be produced. In animals which possess nervous systems, true learning is probably always the result of alterations in the connections between the elements of that system, such that the nervous process is able to pass easily in a direction where it originally encountered high resistances.

The fundamental law of all learning is the Law of Repetition, whereby when a nervous process traverses a certain pathway in the nervous system, it leaves the resistances in that pathway less than it found them. This is the law in accordance with which, when we wish to learn anything,

we repeat it over and over, relying on the certainty that each repetition will make the next one easier. With this law in mind as an essential postulate, we shall survey the types of true learning found in the lower animals under the following four heads: (1) learning involving the dropping out of movements; (2) learning involving the formation of series of movements; (3) the recognition of landmarks; (4) learning involving the anticipation of movements.

§ 74. *Learning Involving the Dropping Out of Movements*

Among all the movements which an animal is capable of making, there are some which are closely connected with the great needs of its existence, and others whose connection with such needs is only indirect and casual. The general process of adjustment to environment which has made the animal what he is, has so ordered matters that the vitally important movements are in a state of especial readiness to be performed. The nervous resistances along the pathways leading to the muscles used in these movements are congenitally low. Such responses are what Sherrington (681, p. 229) has called "prepotent reflexes."

Now if we survey all the cases in which an animal learns by experience, we are obliged to conclude that on some principle of economy of energy, *isolated movements which do not bring any consequences of importance to the organism tend to be dropped*, and their places taken by a state of rest. This seems to be the law according to which we ourselves cease to pay any attention to our familiar surroundings. We cease to notice the ticking of a clock, although no adaptation takes place in the ear itself; we sleep undisturbed by the noise of the trolley cars which is distracting to our friends from the country. The spider experimented

on by the Peckhams reacted each day to the sound of a tuning fork by dropping from its web until the sound had been repeated some half dozen times, but after the fifteenth day it would not drop at all (570). Piéron (588, 590) found that snails, while at first responding to shadows by withdrawing the tentacles, on successive days stopped reacting after fewer and fewer trials; and believed he could trace a parallel between the laws of this learning and those of human memory. There is no question in such cases of the reaction's being dropped off in favor of some other reaction. It is dropped off, as it were, by its own weight; simply because it is useless. This same principle seems to enter as a coöperating factor in cases where animals acquire a discrimination between stimuli. The apparent ability of sea-anemones to distinguish between real food and filter paper soaked in food-juice (see page 254) is, as we have seen, ascribed by some to sensory adaptation, but the experiments of Fleure and Walton (228), if their results are accepted, would indicate that true learning is involved. They tested *Actinia* with a scrap of filter paper once every twenty-four hours, placing it on the same tentacles, which usually carried it to the mouth, where it was swallowed and later ejected. After from two to five days the mouth would no longer swallow the fragment, and in two more days the tentacles refused to take hold of it. Other tentacles could be "deceived" at least once or twice after this, but very soon manifested the inhibition. All traces of the learning were lost after from six to ten days interval. Another anemone, *Tealia*, learned more quickly than *Actinia*. Again, Herrick (297) found that catfish, when the barbels were touched with a bit of meat, immediately seized it. If a piece of cotton wool were used instead of the meat, they made the

same reaction, but after this experience had been repeated a certain number of times they ceased to respond to the cotton, although they still took meat eagerly. The point which especially concerns us is this: "I rarely," says Her-
rick, "after the first trials, got a prompt gustatory reflex with the cotton." The learning persisted for a day or two. The axolotl learned in a similar way to discriminate between pieces of meat and pieces of wood (276). Hermit crabs, which when young try to take up their abode in all sorts of unsuitable objects, glass balls, for instance, later in life make no such efforts (194).

Whether or not a movement which brings no favorable results will be dropped off and a state of no movement will take its place depends on how strongly prepotent the movement is; *upon the strength*, that is, *of the innate tendency to make it*. In the experiments by Professor Bentley and the writer on color discrimination in the creek chub, our first method failed because it required the dropping off, as useless, of a strongly prepotent reaction, and the substitution of no response at all. Red forceps and green forceps, each containing food, were plunged one at a time into the water; the fish was allowed to get the food from the red forceps, but the green ones were withdrawn before it had a chance to bite. The time which the fish took to rise and snap at the forceps was measured by a stop-watch, and in the course of 131 experiments the fish had not learned to rise to the green any less promptly than to the red. In other words, no tendency to drop off the useless movement of rising to the green was detected, although later experiments showed that the fish could distinguish between the two forceps. The movement of rising to and biting any small object in the water was so vitally important to the fish that it could not be dropped off (757). On the other

hand, Thorndike (708) successfully carried out this kind of training with Cebus monkeys: both of his subjects learned to come down to the bottom of the cage for food when the experimenter took the food in his right hand, and to *stay up* when he took it in his left hand, the food being withheld if the monkeys came for it in the second case. Cole (134) trained raccoons to climb up on a box for food when one of two differently colored cards was shown, and to *stay down* when the other one appeared, by not feeding the raccoons if they climbed up for the wrong card.

The dropping off of movements takes place with more speed and certainty if they are made to give place, *not simply to a state of no movement at all, but to a movement of greater prepotency than their own*. Especially effective in thus causing the elimination of a movement is the *negative reaction* of withdrawal from injury. Thus if a movement *A* results in actual harm to the organism, the harmful stimulus thus produced brings about the negative response; and the negative reaction is as a rule prepotent over all others. The next time the movement *A* is initiated, the negative reaction is also initiated, and being prepotent, it is able to check effectively the performance of movement *A*. Thus we have the *dropping off of harmful movements*, a process which is in evidence whenever punishment is used in studying the learning power of animals. It also appears when a successful negative reaction permanently takes the place of unsuccessful ones. We saw in the first part of this chapter that when an animal is repeatedly subjected to a strong and harmful stimulus, it goes through a series of reactions, all directed to getting rid of the stimulus, until one is finally successful. Now if this process is shortened in successive trials, so that the successful negative reaction comes to be made at once and the unsuccessful

ful ones dropped off, we have a case where the dropping off is not simply of useless but of harmful movements (since the unsuccessful ones all result in a repetition of the harmful stimulus); the final state is not one of no movement, but of victory for the successful negative response. A very interesting illustration of this type of learning was obtained from *Paramecium* by Stevenson Smith (688) and by Day and Bentley (178). The method used by these experimenters was fundamentally the same. A glass tube was drawn out until it was so fine that not more than one *Paramecium* could get through it. This tube was filled with water up to a certain point, and a single *Paramecium*, carefully isolated for identification throughout the experiment, was allowed to swim up the tube until the surface film was reached. The animal behaved towards the film as to any mechanical stimulus, darting backward, rolling over towards the side away from the mouth and swimming forward again. Since the tube was so narrow, this method, which ordinarily succeeds in avoiding obstacles, brought the animal against the surface film again. After repeatedly going through the same performance, the *Paramecium* varied its response and succeeded in turning completely around in the tube by bending its body double. On being put again into the same predicament, it gradually diminished the number of trials of the unsuccessful negative response, and arrived at the point where it almost immediately doubled over on striking the surface film. These observations established the existence of a relatively high type of learning in the simplest group of animals.

In this case the movements that are dropped off are themselves negative reactions. In other cases they may be feeding reactions or other responses whose vital impor-

tance, though great, cannot compete against that of the negative response called forth by their injurious effect in the special case. Learning by punishment is in most cases especially rapid. Its effect may be to inhibit altogether, for some time, a certain instinct. For example, the experience of receiving an electric shock when they seized a certain kind of food prevented frogs from feeding at all for several days (657). Rats which were being trained to discriminate between a lighter and a darker passage with the use of an electric shock acquired a distaste for the apparatus as a whole (328). Möbius in 1873 (497) made some experiments with a pike, afterwards repeated by Triplett (720) with perch, which illustrate the same phenomenon. The fish was kept in one half of an aquarium, separated by a glass screen from the other half, in which minnows were swimming about. The pike naturally dashed at them, and whenever it did so bumped its nose on the glass partition. After a considerable period of this sort of experience, the glass screen was removed, and the minnows were allowed to swim freely around the pike, when it was found that the latter's instinct to seize them had been wholly suppressed by the harmful consequences of such action. Here, again, the chances that a movement will be suppressed in favor of the negative response depends on how great the degree of its prepotency is. It was a rash conclusion on Bethe's (49) part to deny the learning ability of the crab because, although every time it went into the darkest corner of its aquarium it was seized by a cephalopod lurking there, it did not in six such experiences learn to inhibit its innate tendency to avoid light: further training would probably have been successful. Yerkes (822) trained an earthworm, by giving it an electric shock when it followed its innate inclination for turning towards

a darkened region, to turn away and towards the light. The cockroach, as is well known, prefers darkness to light: Szymanski (701), however, succeeded, by giving it an electric shock when it ran into the dark part of a box, in educating it to turn back as soon as it reached the edge of the darkened region, without waiting for the shock, and Turner (729) obtained similar results.

When an instinct is thus completely suppressed by punishment, the conscious accompaniment of this modification in behavior is probably simply a change in the affective tone of the situation. Instead of being pleasant, it becomes unpleasant. In a human being, memory ideas might accompany the process: a human pike, for instance, might at the sight of a minnow recall clearly the bump on the nose and his consequent humiliation. But we can explain the pike's behavior just as well if, in accordance with Lloyd Morgan's canon, we assume merely that the sight of a minnow has become unpleasant to him: he has lost his taste for minnows.

Punishment has been the means in many cases of training animals to manifest their ability to discriminate between stimuli. The desired end is of course to attach the negative reaction to those features in which the "wrong" stimulus differs from the "right" stimulus. For instance, an animal is being taught to choose a light rather than a dark passage, the two openings being side by side: when he enters a dark passage he gets an electric shock. It will be natural for him at first to attach the withdrawing reaction consequent on the electric shock to the sight of the whole apparatus. Whether he will shrink back from it or rush indiscriminately into either of the passages depends on the relative prepotency of his impulse to enter the passages and his impulse to withdraw from injury: in either

case he makes no discrimination. The discrimination occurs when the withdrawing reaction attaches itself to the feature which distinguishes the dark passage from the rest of the apparatus, namely, its darkness. It is probable that in many cases the animal does not deliberately compare the light with the dark passage, but merely learns to distinguish the passage to be avoided from the rest of the situation at large. We should expect this to be the case where punishment is the only method of training used: the case would not be one of "white preferred to black," but of "anything rather than black."

The strength of the punishment applied is of course an influential factor in the learning. Obviously it depends not merely on the strength of the punishing stimulus, but on the sensitiveness of the punished animal. Yerkes was the first experimenter to employ the electric shock as a means of training animals. He used it on the frog (805), which he was trying to educate to make a turning to the left rather than to the right: the frog showed a discouraging tendency to sit motionless for long periods of time, and so Yerkes placed electric wires on the floor, to induce by a mild shock greater activity. In his work on the dancing mouse (820), he substituted the giving of electric punishments in the case of wrong choices, for the older method of rewarding an animal's right choices, and one of the advantages claimed for this method was that it seems to allow an exact measurement of the strength of the stimulus, whereas a reward, such as food, varies in strength with the animal's physiological condition. But the effect of an electric shock too varies with the temporary physiological state of the animal, and with its general individual sensibility. Yerkes (827) carried out some interesting experiments on the relation of the strength of the punishment to the difficulty

of the discrimination required of the animal. A superficial consideration of the situation might assume that if one wants to teach an animal a difficult discrimination, such as that between two slightly different shades of gray, one ought to supply a stronger punishment stimulus than would be necessary to teach it an easy discrimination, such as that between black and white. The results with the dancing mouse showed on the contrary that weaker punishments were more effective in the learning of hard discriminations; stronger punishments in that of easy discriminations. The same rule was found by Dodson to hold for cats (186 a); the hardest discriminations were acquired by kittens in 82.5 trials with a moderate stimulus, but 107.5 trials were required on the average with a strong stimulus. Indications of a similar relation were found by Cole (136) in the learning of chicks.

The negative reaction is not the only one which may show sufficient prepotency to cause the dropping off of other responses. The feeding reaction, or any other innate response, may serve: thus *reward* as well as punishment is a method of training. The taming of an animal by kind treatment illustrates both the simple dropping off of useless movements, the getting used to a situation, and the substitution of movements more valuable to the animal; the tamed creature on the one hand learns to rest quietly in the presence of its tamer, instead of displaying alarm, and on the other hand to come for food or follow for companionship. A very pretty illustration of the overcoming of an innate response to light by the response to feeding was obtained by Wodsdalek (795) on immature mayflies. These insects have an innate tendency to avoid light and to remain under stones in the water. By regularly feeding them on the upper surface of a stone the

experimenter was able wholly to overcome this reaction, especially with one gifted individual. After two months of training, "all that was necessary to bring the specimen up when it had disappeared from sight was to slightly jar the dish or the table on which the dish was located, and the insect would quickly come up to the upper side of the rock and make for its feeding place." Here again, the conscious aspect of the learning is probably a reversal of the emotional tone of the situation: originally unpleasant, it has become pleasant. Where the method of reward is used to train animals in discriminating stimuli, the influence of the reward is combined with that of the tendency to drop off useless movements. Cole's raccoons learned not only to climb up when the food signal was given, but to stay down when the no-food signal appeared. The rabbits studied by Miss Abbott and the writer (756) were taught to push at a door carrying a piece of red paper, and to refrain from pushing at a door carrying gray paper. The original stimulus for the pushing was the odor of food which was in the compartments behind both doors. The "gray" door was always bolted on the inside, so that pushing against it was in vain; the "red" door opened freely so that the rabbits could get at the food. The actual securing of the food acted, along with the smell of it, to suppress all useless hesitations on the part of the animals and to make them more inclined to push the doors at once; the gray stimulus acquired a tendency to lose its motor effect because the movements to which it gave rise were useless.

So-called "puzzle-box" experiments also depend for their training effect upon the combined tendencies to the survival, through their prepotency, of movements resulting in the satisfaction of an instinct, and to the dropping

off of useless movements. The method has been tried with birds, rats, squirrels, cats, dogs, raccoons, porcupines, and monkeys. Thorndike, its originator, made some experiments of this type on chicks confined in pens from which they could be released by pecking at a string or some such object (704). Porter tested English sparrows with boxes containing food, which could be en-

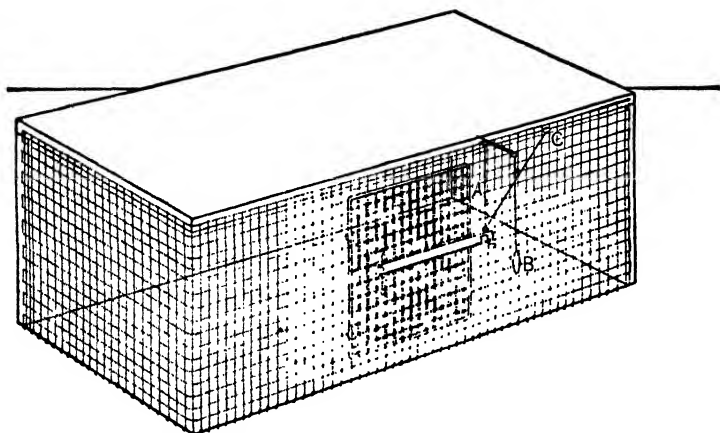


FIG. 12. -- Puzzle box used in Porter's work on birds; *AB*, one method of attaching string to latch; *C*, a second method. In the first, the loop at *B* had to be pulled; in the second, the string had to be pushed in.

tered by pulling a string fastened to a latch, or by pushing the string into the wire netting with which one side of the box was covered (Fig. 16). The sparrows learned very quickly; one of them by the tenth test had left out all unnecessary movements (610). In later experiments a cowbird and a pigeon also learned to open a similar box. Before beginning the test the birds were accustomed to being fed in the box with the door open. Their first success in opening the door lay in accidentally clawing or pecking at the proper point, and in later trials the action

was simplified; thus the birds learned not to attack other parts of the box, to use the bill instead of the claws, and to stand on the floor beside the box instead of hopping upon it (611). In Rouse's test of the pigeon by the puzzle-box method, it showed less aptitude than that displayed by the English sparrow (647).

Small (684) tested his white rats with two boxes containing food. One could be entered by digging away the sawdust which was banked around the lower end of the box, if the digging was done in a particular place; the other, by tearing off strips of paper which held shut a spring door. The result of the earlier series of experiments with the first-mentioned box was that after an hour and a half on the first day one rat happened to dig in the right place and entered. The second day this rat took only eight minutes, and the thirteenth day only thirty seconds, to enter. With the second box there was always a tendency to begin by digging, and even in the thirteenth experiment, where the rat got in by biting off the papers in fifteen seconds, she began by two strokes of digging. In a later test with this box the rat chanced to be extremely hungry, and dug violently for several seconds, displaying a blunting of the discriminative powers by hunger, analogous to that which we have found in very low animals. The rats were later trained to discriminate between the two boxes, being sometimes presented with one and sometimes with the other.

In Thorndike's work on cats and dogs, the investigator placed the animals themselves in the boxes, and food on the outside, so that the problem was not how to get in but how to get out. The getting out could be accomplished in various ways, such as pulling a wire loop, clawing a button around, pulling a string at the top of the box, poking

a paw out and clawing a string outside, raising a thumb latch and pushing against the door, and so on (Fig. 13). The animals, on being first put into the box, made all sorts of movements in their struggles to get out; the right movement was hit upon by accident. Only very gradually, as the experiment was repeated again and again, were the useless movements omitted, until finally the right one was

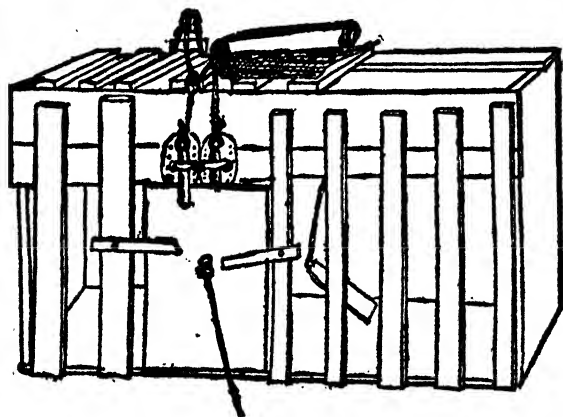


FIG. 13. — Puzzle box used in Thorndike's experiments on cats.

performed at once (704). Wesley Mills criticised these pioneer experiments of Thorndike's on the ground that the animals were under such unnatural conditions and in such an extreme state of hunger that they profited by experience more slowly than might otherwise have been the case (492); and this may have been to a certain extent true. In testing monkeys with puzzle boxes Thorndike placed the food on the inside and the monkeys on the outside. He found a marked difference between the speed of their learning and that shown by the cats and dogs. "Whereas the latter were practically unanimous, save in the cases of the very easiest performances, in showing a process of

gradual learning by a gradual elimination of unsuccessful movements and a gradual reinforcement of the successful one, these are unanimous, save in the very hardest, in showing a process of sudden acquisition by a rapid, often apparently instantaneous abandonment of the unsuccessful movements and selection of the appropriate one, which rivals in suddenness the selections made by human beings in similar performances" (708). Kinnaman further complicated the box tests with his *Macacus* monkeys by constructing "combination" fastenings, which required the performance of a set of actions in a certain order, and found that these were mastered by the animals (401) (Fig. 14).

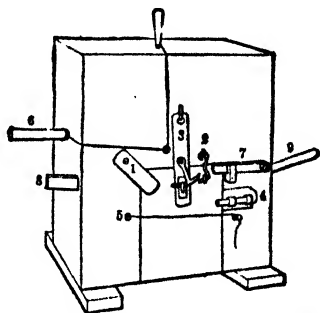


FIG. 14. — Combination fastening used in Kinnaman's work on monkeys. The figures indicate the order in which the parts of the combination had to be dealt with.

Cole's (134) work on the raccoon indicates that in speed of learning this animal stands "almost midway between the monkey and the cat," while "in the complexity of the associations it is able to form it stands nearer the monkey." The raccoons, like the monkeys, learned combination locks, although they did not learn to perform the various movements involved in a definite order. They showed an interesting tendency to skip at once to the movement that immediately preceded the opening of the door. The porcupine also proved gifted with the ability to learn combination locks (651), while the squirrel's puzzle-box exploits were limited to boxes which could be entered by the simple process of digging in sawdust (832). The learning

of combination locks probably involves the formation of systems of movement, as well as the dropping off of useless movements; the process of system formation will be discussed in a later section.

The building up of systems of movements is an important part of the learning process in another method of studying

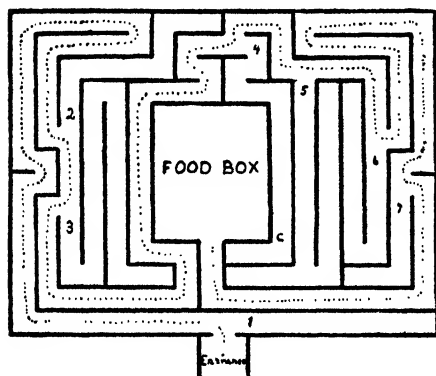


FIG. 15 — The Hampton Court maze.

the intelligence of animals, namely, the labyrinth or maze method. In the typical form of this method, food is placed at the end of a pathway involving a number of turnings, in which it is possible to make errors of two sorts: (a) taking a longer instead of a shorter route, (b) entrance into *cul-de-sacs*. The animal has to learn to run to the end of the path and secure the food in the shortest possible time, or by the most direct route. His progress in learning may be measured either by the total time he consumes in running the path in each trial, or by the number of errors he makes, or by the total distance he runs. The method in its developed form was first used by Small (685) in experiments on white rats, and is especially adapted to an animal so active as the rat. Small used a very complicated maze, a facsimile on a small scale of the one to be found in the grounds of Hampton Court Palace (Fig. 15). Such mazes, with high box walls, were a frequent feature of old gardens. Much simpler mazes have been used with other

the intelligence of animals, namely, the labyrinth or maze method. In the typical form of this method, food is placed at the end of a pathway involving a number of turnings, in which it is possible to make errors of two sorts: (a) taking a longer

animals. Where a maze consists of only two passages, requiring the animal to learn merely a single turning, the method may be practically merely a discrimination method: thus Yerkes's (822) training of the earthworm made use of a maze with two passages only to choose between, a light and a dark one. In a pure maze experiment, however, there is no way of distinguishing between the passages except by experiencing the consequences of following them. Thus the crayfish was tested by the use of a maze with a single choice of paths. One end of the box communicated with the aquarium; about halfway down the length of the box a partition put in longitudinally divided it into two passages, one of which was closed at the end by a glass plate. In sixty trials the animals, which had originally chosen the correct passage 50 per cent. of the time, came to choose it 90 per cent. of the time. A second series, with a single animal upon which more tests a day were made, resulted in the formation of a perfect habit in two hundred and fifty experiments. The glass plate was then shifted to the other passage, and the crayfish was naturally completely baffled for a time, but succeeded in learning the new habit (829). The crab *Carcinus granulatus* made progress in learning to traverse a labyrinth with two points where a choice of path had to be made, but did not wholly master it in fifty trials (804). For both the crab and the crayfish, the experience of getting back into the water was the influence relied upon to eliminate the useless movements; the slow learning of these animals indicates that the method was not well adapted to them. Ants showed some ability to learn a maze with several turning points, following the proper course even when their smell trail was obliterated (219). Fish have proved able to learn very simple labyrinths, but have not been tested in complicated ones (705, 121).

With the green frog, a maze allowing two choices was used, and was learned in one hundred trials (805).

With the turtle, a labyrinth distinctly more complex was used. It involved four blind passages, and led to the turtle's comfortable, darkened nest. During the first four trips the time was reduced from thirty-five

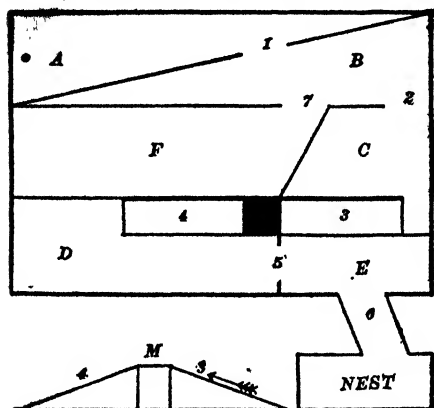


FIG. 10. — Labyrinth used by Yerkes with turtles. A, starting point; F, blind alley; 3, 4, 6, inclined planes.

minutes to three minutes and thirty seconds; in the fourth trip the animal took two wrong turns. The time of the fiftieth trip was thirty-five seconds. In a second labyrinth (Fig. 16), two inclined planes were introduced, up and down which the turtles had to crawl. This labyrinth took

them longer to traverse, and the time curve shows greater irregularity, rising, for instance, to seven minutes on the forty-fifth trial, after having been as low as two minutes and forty-five seconds at the thirty-fifth. The process of shortening the path was observed very prettily in connection with the inclined planes. The turtles had to turn about as soon as they had reached the bottom of the descending plane. They soon began to make the turn before they got to the bottom, and finally to throw themselves over the edge as soon as they reached the top (801).

Some of Thorndike's (704) early experiments on chicks involved a very simple form of the labyrinth method, in

that the chicks, which were confined in small pens, could escape by running to a particular spot, or up an inclined plane. Porter (610) found that the English sparrow quickly learned the Hampton Court maze, and that the vesper sparrow and cowbird learned a simpler form in twenty or thirty trials (611). Pigeons tested by Rouse acquired the ability to traverse four different labyrinths, and it was noted that their experience with the earlier ones seemed to help them in the later ones (647). Hunter's (349) experiments on the pigeon with the use of the maze will be mentioned later.

White rats observed by Small learned the Hampton Court maze, in nine experiments made at intervals of two days, so well that they committed only two errors in the ninth test, but the significance of this time is obscured by the fact that the rats were allowed to run freely about the labyrinth every night (684).

In Yerkes's (820) study of the Japanese dancing mouse, the reactions to irregular and to regular labyrinths were compared, and it was found that a maze of the latter type, that is, one where left and right turns alternated, was more quickly learned and more perfectly mastered than an irregular one. Kinnaman (401) taught two *Macacus* monkeys the Hampton Court maze.

The feature of maze learning which interests us at this point is the dropping off of useless movements. This probably occurs partly through the general tendency of useless movements to be omitted, and partly through the tendency of the successful movements to survive. It has been argued that if the shortening of the maze running is due to the fortunate consequences of the successful movements, then the errors which should be earliest dropped off are those at the latter part of the course, which come nearest in point of time to the final success, usually the

obtaining of food. Hubbert (346) does not find that this is actually the case, but Vincent (750) does, and on the whole the evidence points to the conclusion that the errors nearest the final success are the first ones eliminated. Such exceptions to this tendency as appear may well be due to two causes: first, the natural tendency of useless movements to drop away even when a successful movement is not pushing them out, and secondly, the equally natural but wholly opposed tendency of movements to organize themselves into systems, a tendency which will be considered in the next section. Watson (771) lays especial stress on the fact that the successful movements in puzzle-box and maze experiments have the advantage of frequency of performance. The successful movements are always performed, in every maze experiment, simply because the experiment continues until they are performed; there is no such necessity that any particular unsuccessful movement should be performed in every experiment. Thus the successful movements, Watson thinks, owe their survival to the law of repetition. It is quite probable that their inevitable performance once in each running of the maze may be a factor aiding their survival, although quite conceivably, as Thorndike¹ has suggested, many unsuccessful movements may actually be oftener performed, owing to the fact that they may be repeatedly tried in the same experiment. But Watson endeavors to reduce all learning through the dropping off of movements to the influence of the frequency with which the successful movements occur; and this can only be done by ignoring such cases of learning as those where the frog ceased in one or two trials to snap at food when the snapping led to harmful consequences, or where the spider learned not to disturb itself at the sound of a

¹ Jour. Animal Behav., vol. 5 (1915), p. 465.

tuning fork. Frequency cannot be a factor of importance here. Such cases show that there do exist in animals tendencies (*a*) to abandon movements which have no consequences of importance to the organism, and (*b*) to eliminate even movements that are important in favor of movements that have greater importance. It is not clear why Watson is unwilling to admit that the "sensory consequences," the vital importance of the results of a movement, are factors in determining its survival. He seems to think that sensory consequences must be stated in terms of mental processes, and therefore must not be mentioned by a consistent "behaviorist." We, not being behaviorists but psychologists, are quite willing to talk about the pleasantness and unpleasantness accompanying the benefit and harm of reactions, but if we were behaviorists, we should certainly not feel obliged to deny that animals can be benefited or harmed by their own actions, because we feared benefit and harm might suggest pleasantness and unpleasantness to the minds of our readers.

Before we pass on to another aspect of learning, which is quite as important in the phenomena of maze running as the dropping off of movements, there are a few points to be noted with regard to the relation between punishment and reward, harm and benefit, as influences in learning. Punishment appears to produce more rapid learning than reward, unless it is so severe that it attaches itself to the whole learning situation. Punishment and reward combined give, probably, better results than either alone (328). Further, a movement that results in harm, and is therefore supplanted by the negative response of withdrawal, is more completely eliminated than one which is merely useless and is supplanted simply by a state of rest. Evidence of this was obtained by Bogardus and Henke (59) in experi-

ments where, after rats had learned a maze, the path was altered, certain passages being closed and others opened. The rats found it decidedly harder to learn to enter former *cul-de-sacs* than to take those turnings which they had formerly omitted merely because they were a longer way around than the true path. The positively unpleasant experience of running into a *cul-de-sac* had more completely eliminated the movements that led to it than did the merely useless running of a longer passage. Finally, it is clear that we cannot draw a hard and fast line between a useless reaction and a harmful one. We have seen that a severe punishment like an electric shock may delay learning because it attaches itself to the learning situation as a whole. And in the writer's experiments with rabbits (756), a young rabbit of very nervous temperament was rendered unfit for further experimentation simply by happening to push repeatedly at the wrong or closed door of a box. He had been working well up to that time, but from that time on he ran away whenever he was confronted with the experiment box. It would appear that emotional factors in the animal may render movements positively harmful which would ordinarily be merely useless.

§ 75. *The Formation of Systems of Successive Movements*

We have now to consider another type of learning, diametrically opposed to that of the dropping off of movements. In this type, the movements which an animal makes successively become organized into a series. No movement of the series is dropped out as a result of the learning, but the oftener the series is run through, the more rapidly it is performed. It is evident, if we consider our own learning processes, that many of them are of this type. When we

say the alphabet or the multiplication table, the learning process has not involved the dropping out of any of the movements. It would profit us little to pass immediately from A to Z, dropping out the intervening movements, or to skip at once from the first to the last stanza of a poem. We find in such cases that repeated performance of the series of movements results in two changes. First, the movements follow each other more rapidly: this can be explained by the law of repetition, according to which the oftener the nervous process traverses a certain pathway, the less resistance it encounters. Secondly, the movements of the series no longer need outside stimuli, but apparently each movement supplies the stimulus for the next. When one is playing a piece of music for the first or second time, each movement has to have the stimulus of the notes on the page; when a piece has been long practised, each movement sets up the next one 'automatically.' This really means that as one movement is performed, the sensory processes occasioned by the contraction of the muscles involved excite the motor pathway for the next movement. The stimulus for one movement is the kinæsthetic excitations received from the preceding movement. The truth of this is evidenced by the fact that if we break down in playing a certain passage, we can recover ourselves by going back a little, so as to get the proper kinæsthetic stimuli.

This type of learning obviously functions in learning a maze path. Here we have to deal not with the acquiring of a single 'successful' movement and the dropping off of all others, but with the establishment of a whole series of successful movements which must be performed in a certain order. Much experimentation has been performed to study the sensory cues involved in maze running. The

question resolves itself into three: (1) What sensory stimuli does an animal rely upon after it has thoroughly learned the maze path? (2) What sensory stimuli does an animal naturally rely upon in learning the maze path? (3) What sensory stimuli can an animal do without, if necessary, in learning a maze path?

(1) All the evidence indicates that when a rat has thoroughly learned the maze, its movements have become organized into a system such that the sole requisite stimulus for the performance of one movement is the kinæsthetic excitation resulting from the preceding movement. The best proof of this is furnished by experiments where the rats which had learned the maze from its beginning were started at points further along; they could not pick up the true path with any speed until, in running back and forth, they chanced to make two or three correct turnings. This set off the remainder of the maze-running process precisely as playing over the preceding passage would enable a pianist to proceed beyond the point of a breakdown. Similarly, when the maze was shortened by removing a section from its middle, the rats ran against the ends of the shortened passages; when it was lengthened by elongating certain passages, the rats tried to make the turns at the old points (118).

(2) and (3) It is difficult to make sure just what sensory stimuli function in enabling an animal to learn the maze. The only methods that suggest themselves are (a) that of depriving an animal of the use of one sense and seeing whether he can learn the path, thus answering question (3) above; or (b) that of supplying him with cues especially appealing to a certain sense, and noting whether his learning is accelerated. But neither of these methods reproduces the condition of normal maze

learning. Watson (767) showed that rats deprived of sight, hearing, smell, and touch (the vibrissæ or long whiskers being removed and the paws made anæsthetic), could learn the maze. Yerkes (820) demonstrated that the Japanese dancing mouse does not necessarily depend on sight, smell, or touch for guidance. On the other hand, Vincent's (747-749) experiments show that a maze in which the true path was painted black and the wrong paths white, or *vice versa*, was learned more quickly than an ordinary maze; that one in which the true path was smeared with beef extract and cream cheese alternately (the two odors being used to prevent olfactory adaptation) gave a greater total accuracy; and that in a maze without sides, that is, an elevated pathway, the rats were much disturbed by the loss of the accustomed contact with the walls. Different animals are undoubtedly unlike in the use they make of sensory cues. The frog studied by Yerkes (805) in a very simple labyrinth showed a disturbance in its habit when red and white cards placed on either side of the passage were interchanged. The pigeon (647), when required to go through a labyrinth in darkness, was obliged to relearn it. On the other hand, Small found that altering the direction of the light had little effect on the performances of his white rats. He also placed wooden pegs painted red, at each division of the paths, in the middle of the correct path, and caused the maze thus arranged to be learned by untrained rats. They did not learn it any faster because of the presence of these visual hints, nor, when it had been learned, were they at all discomposed by the removal of the pegs (684). Allen's (4) guinea pigs did not alter their behavior when the position of colored cards in the maze was changed. Rouse (647) found that the pigeon could make use of auditory stimuli as cues. He arranged to have

an electric bell rung whenever the birds entered a wrong alley, and a wooden bell sounded when they emerged and took the right course. After they had learned the path under these conditions the two kinds of sound stimuli were interchanged, and the result was a certain amount of confusion on the part of the birds. On the whole, in the case of active animals whose vision is not highly developed, such as the rat, the principal factor in learning a maze appears to be the actual running of it. As the paths are traversed at random, the useless movements tend to be dropped off, and the successful ones not merely to survive, but to become organized into a system such that each movement itself provides the stimulus for the succeeding one. Vincent (747) found that while visual cues aided the learning of the maze, the final running was not so rapid as if the habit had been formed wholly under kinæsthetic guidance.

Some curious results have been observed when the maze is rotated through angles of 90, 180, or 270 degrees. Since this has no effect on any of the paths, but only on the relation of the entire maze to its environment, it ought not to disturb animals which are depending entirely on their own movements for their cues, yet apparently it does in some cases disturb them (767). Possibly the preliminary swings which the animal gets in being picked up and introduced to the entrance of the maze are the disturbing factor. Hunter (349) found that some of his pigeons were disturbed when the maze was rotated, while others were not, and concludes that the latter were guided by cues within the maze, the former by cues from without.

Maze experiments are not the only observations on animals which reveal the existence of successive movement systems, or "kinæsthetic memory." If Piéron (579) is

'right, some species of ants are aided in their return to the nest by repeating all the turnings they took on the outward journey. Watson reports the following observation on the terns of the Tortugas. On an occasion after he had trained one of these birds to use a nest raised a hundred centimeters above the ground, he moved the nest a hundred centimeters to the eastward; the bird, returning, hovered "in space, attempting to adjust to the nest in the air at its former position and height" (769, page 226). Rockwell (639) relates that a ground squirrel had made inside a cabin, a nest which it was accustomed to reach by climbing up the leg of a cot that stood in one corner of the cabin. When the cot was removed, the squirrel, entering the cabin, ran to the place formerly occupied by the cot, and went through the motions of trying to climb the non-existent leg.

It must further be noted that useless movements not infrequently get organized into movement systems, and thus their elimination is delayed. Animals in running a maze form habits of going wrong which greatly interfere with the reduction of their time records. In the case of some salamanders which the writer vainly tried to teach a fairly complicated maze, each individual acquired quite an elaborate habit of making wrong turnings, and remained true to it for some time. Whenever the situation does not involve strongly prepotent movements, whenever, that is, the "motive" is weak, the natural tendency of movements to organize into systems may take the place of the tendency to drop off the unnecessary ones. Such an influence as this is very likely one reason why errors in the maze are not eliminated in the exact order of their distance from the final, beneficial, and pleasurable goal.

The conscious accompaniment of the formation of suc-

cessive movement systems is, in our own experience and probably in that of an animal, the diminishing of attention to outside stimuli, and the disappearance of such emotional states as uncertainty and the unpleasantness of errors; a feeling of confidence and security replacing them.

There is an alleged case of learning on the part of certain marine animals which, if it exists, probably belongs under the head of the formation of successive systems. This is the acquisition of rhythmic reactions, to stimuli which occur at equal time intervals, and the persistence of such rhythms when the stimuli have ceased to act. Marine snails, sea-anemones, annelid worms, and hermit crabs show changes in the direction of their responses to light and to gravity which correspond with the state of the tides: the sea-anemone, for instance, opens at high tide and shuts at low tide. Now certain French observers, Bohn (80, 90), Piéron (584), and Drzewina (192) report that when the animals are removed to the aquarium, they continue to show fluctuations in their light and gravity reactions at the times of high and low tide, although of course the actual stimuli which the tide gives them, for instance the mechanical jarring of the waves entering their pool as the tide rises, are now wholly lacking. No American observer has been able to show such a continuance of the tidal rhythm in animals removed from direct tidal action (256, 293, 509 a, 551). The phenomenon suggests analogies from our own experience; for instance, there is the case of "habit hunger." We feel hungry at the time of day when we are accustomed to be fed; if we do not get food at this time, in half an hour or so the hunger sensations disappear, and we can go quite comfortably without food for some time longer. The hunger sensations are due to movements of the stomach; now these movements were originally in-

duced by the presence of food in the stomach at a certain time. They have apparently become a part of a system of internal, organic movements, so that when these internal processes have continued for a length of time equal to that which usually elapses between meals, they produce the stomach contractions, in the absence of the original stimulus, the food. Thus the case seems to be like that of the running of the maze by a thoroughly practised animal; each act is the stimulus for the next, and outside stimuli are unnecessary.

CHAPTER XI

THE MODIFICATION OF CONSCIOUS PROCESSES BY INDIVIDUAL EXPERIENCE (*Continued*)

§ 76. *The Recognition of Landmarks*

A TYPE of learning which stands by itself is that involved in the homing of certain animals. As we have seen, the evidence is conclusive that solitary wasps guide themselves back to the nests they have made by "recognizing" certain visual peculiarities of the surroundings. They are confused if the appearance of the nest or its vicinity is altered. On first leaving the nest in search of the prey with which to stock it, as food for the larva, they make an elaborate flight with many turnings in and out about the immediate neighborhood, which has been appropriately termed a locality survey. Now when the wasp has found and secured the caterpillar or spider which she seeks, she retraces her flight apparently with the guidance of the visual landmarks she noted on the outward journey. No one, it is true, has yet actually determined the homeward flight of the wasp in its relation to landmarks, but the probabilities are that such is her method of procedure. The peculiarity of such learning is that it does not depend on repetition. The wasp makes but one nest in a given situation, and in the case of certain species at least she makes but one flight in search of food and but one homing flight. She then makes a new nest in a new locality, impresses new landmarks upon her memory, and is guided in her next

homing flight by the new and not the old landmarks. The learning is essentially rapid and temporary. Where, as for instance with the honey bee, the nest remains permanently fixed in one locality, guidance by visual landmarks does not differ from the ordinary types of learning where the process is gradual, where useless movements are eliminated and useful movements organized into systems. We are still in possession of too few detailed observations on the homing flights of the wasp to draw positive conclusions as to the nature of the learning process here.

§ 77. *The Memory Idea*

It is sufficiently clear that animals possess the power of learning, in the sense of a power of reacting differently to a present stimulus because of their past experience with it. Probably not a single animal form is so low that it lacks this power. But there is another type of learning, of which human beings make much use, whose existence in animals we have yet to investigate; namely, the ability to recall a mental image of an absent stimulus, a memory idea. A dog shows clearly that he remembers his master, in the sense of modifying his behavior in his master's presence because of his previous experience. Can we be sure that he has remembered him in his absence; that he has had a memory image of his master?

Most people, following the tendency to humanize animals and ignoring Lloyd Morgan's canon, interpret as evidence of memory ideas certain features of animal behavior which are susceptible of much simpler interpretations. Dogs and cats, for instance, are supposed to dream because they snarl and twitch their muscles in sleep; but as Thorndike (704) has pointed out, such movements may be purely

reflex and unaccompanied by any consciousness whatever. A dog shows depression during his master's absence, but his state of mind may be merely vague discomfort at the lack of an accustomed set of stimuli, not a clear idea of what he wants; as when we feel that we have forgotten something or that something in our environment has been altered.

We shall first consider certain pieces of evidence which indicate that in many of the lower animals the existence of memory ideas is highly doubtful. Later, we shall note certain testimony in favor of their existence in the minds of some animals, although probably with a very restricted function.

One argument from which we may conclude that animals do *not* make use of memory ideas where human beings would, is derived from the *gradual character* of the dropping off of useless movements in experiments of the puzzle-box type. A human being who had once hit by accident on the right way to open a lock could hardly fail, on being confronted with the lock a second time, to recall an idea of the successful movement, and to perform it at once, without wasting time and effort on unnecessary movements; but a dog or a cat makes almost as many random clawings and pawings the second time as the first, and only gradually omits the irrelevant motions.

In the next place, animals very generally show a *lack of ability to imitate other animals when the "imitatee" is not actually present* before them; they cannot imitate by remembering another animal's movements. Imitation may be, as various authors have pointed out, of at least two different types. The first may be called *instinctive imitation*, and is widespread throughout the animal kingdom. It occurs when the sight or sound of one animal's performing

a certain act operates as a direct stimulus, apparently through an inborn nervous connection, to the performance of a similar act by another animal. "If," says Lloyd Morgan, "one of a group of chicks learns by casual experience to drink from a tin of water, others will run up and peck at the water and will themselves drink. A hen teaches her little ones to pick up grain or other food by pecking on the ground and dropping suitable materials before them, the chicks seeming to imitate her actions. . . . Instinctive actions, such as scratching the ground, are performed earlier if imitation be not excluded" (507, pp. 166-167). Imitation in this sense is hardly so much a method of learning by experience as a method of supplying experience. An animal may perform an act the first time because, through inherited nervous connections, the sight of another animal's performing it acts as a stimulus. But it will continue to perform the act, in the absence of any copy to imitate, only if the act is itself an instinctive one, like drinking in birds, or becomes permanent by reason of its consequences, just as would be the case if its first performance had been accidental rather than imitative. As a matter of fact, instinctive imitation seems usually to be concerned with actions themselves instinctive.

Inferential imitation, or what Morgan calls *reflective imitation*, is a different affair. It is the case where an animal, watching another one go through an action and observing the consequences, is led to perform a similar act from a desire to bring about the same result. Such behavior naturally suggests that it is accompanied by some kind of memory idea of the action that is imitated. Now Thorndike, in his experiments on chicks, cats, and dogs, found no evidence of this type of imitation. A cat put in a puzzle-box did not learn the way out any sooner for watching,

even repeatedly, the performances of a cat that knew how to get out (704). With monkeys, Thorndike's most extensive tests were made to find whether the animal would learn to open a box from seeing the experimenter himself do it, and his results were again, on the whole, negative (708). Small's white rats also showed no ability to profit by each other's experience in this way. One of each of the pairs first experimented on solved the problems presented; the other, instead of either attacking them for itself or learning by watching the successful one, contented itself with stealing the food secured by the latter (685). Imitation, according to Yerkes, plays no considerable rôle in the learning processes of the dancing mouse (820). Where an animal is not at all helped to the solution of a problem by watching another animal solve it, we are justified in concluding that if it can recall memory ideas at all, it does not make use of them in a situation where a human being would certainly do so.

The lack of ability on an animal's part to postpone reacting to a stimulus is another evidence of inability to make use of memory ideas. The very ingenious method by which such ability may be studied was the device of Hunter (350). It has been termed the Delayed Reaction Method, and its general plan is as follows. A light is shown for a few seconds in any one of three directions from the animal, which is restrained from reacting. After the light is turned off and a certain time interval has elapsed, the animal is released, and if it goes in the direction in which the light appeared, it receives food. Now white rats could succeed in running in the proper direction when the delay between the disappearance of the light and their release was not more than ten seconds, but only in case they pointed their noses at the light when it appeared and

remained motionless in this position during the interval. Clearly we get no indication from such behavior that the rat is able to recall a memory image of the light. His failure to run in the right direction when he did not keep his nose pointed in the right direction plainly suggests the absence of such ideas as influences on his behavior.

Again, the *nature of the errors* which animals occasionally make in experiments strongly suggests the absence of memory ideas. Thus the two rats which learned the Hampton Court maze under Small's (685) tuition both continued, after they had reached their highest point of excellence in running the maze, to take the wrong turning at the outset. Precisely this error would have been, probably, the first one eliminated in the learning of a human being, who would be able to recall some kind of memory idea of the first turning owing to its especial hold upon attention. Further, the *way in which instinctive actions are often performed* by animals indicates that ideas are not present as they would be to a human being's consciousness. Human beings do some things from instinct, but the doing of them may be accompanied by ideas; a mother's care for her child involves ideas of the child's happiness or suffering, and of its future. Enteman's account of the worker wasp which, lacking other food to present to a larva, bit off a portion of one end of the larva's body and offered it to the other end to be eaten, suggests a peculiar limitation of ideas in the wasp's mind, at least while this particular function was being performed (206). The cow, which had lamented at being deprived of her calf, and on having the stuffed skin of her offspring given to her, licked it with maternal devotion until the hay stuffing protruded, when she calmly devoured the hay (504, p. 334), had perhaps experienced some dim ideas connected with her loss, but certainly her con-

sciousness was more absorbed by the effects of present stimulation and less occupied with ideas than a human mother's would have been.

Thorndike (704) was the first to point out how scanty is the evidence in favor of the possession of ideas by the lower animals. In addition to the fact that his dogs and cats dropped off their useless movements so slowly, he adduced the observation that while after a time the cats which had been caused to enter a puzzle-box and let themselves out before being fed would of their own accord go into the box, cats that had been from the first dropped into the box at the top never learned to go in of their own accord. He argued that if a cat had been able to have the idea of being in the box, as a necessary prelude to food, it would have been able to pass from the idea of being dropped in to that of going in itself. This argument, however, is not fully convincing. The experience of being picked up and dropped into a box is very different from that of walking through a door. To the human mind, accustomed to more refined analysis of its experiences, one of these would suggest the other, but we cannot argue that because such a connection is not made in the animal's mind, therefore the latter is incapable of ideas, any more than we could conclude a total absence of ideas from the consciousness of a man to whom a primrose by the river's brim does not suggest thoughts of the moral government of the universe. Moreover, several observers have reported precisely this ability to get the habit of jumping into a box from being dropped in; our rabbits (756), which were put into a box for safe keeping between experiments, within two days acquired the trick of running to the box and scrambling into it, the whole experience being a prelude to food.

The same comments, precisely, apply to Thorndike's

observation that his dogs and cats were not helped to learn a puzzle-box mechanism by being put through the movements. The absence of ability to pass from the experience of being put through a movement to the idea of performing the movement is no proof of incapacity to form ideas; moreover Cole (134) found that the raccoon did learn to work a fastening by being put through the movements. Hunter (351) made a similar observation on the rat, and the method seems to meet with success in the hands of animal trainers.

In general, however, we must admit, the facts point to the conclusion that ideas are very rare in the animal mind. We can in some cases, however, present positive evidence of their occurrence. One attempt to demonstrate them, that of Cole (134), it is true, seems hardly conclusive. Cole trained raccoons to discriminate between various stimuli. Cards were placed on levers so that by a touch they could be pushed up and down. The animals learned to climb up for food when one of two differently colored cards was shown, and to stay down when the other one appeared; to distinguish in a similar way between a high and a low tone, between a round and a square card, and between a card $6\frac{1}{2} \times 6\frac{1}{2}$ inches and one $4\frac{1}{2} \times 4\frac{1}{2}$ inches square. Of course the action of climbing up was not itself purely instinctive, but had become associated with the food instinct. The raccoons also hit upon the trick of clawing up the cards themselves, and if the one that appeared was the "no-food" card, they would either claw it down again and pull up the other, or proceed at once to pull up the other, leaving the "no-food" one also up. Since the cards were shown successively, Cole concludes that "remembrance of the card just shown was required for a successful response." "Why," he asks,

"should the animal put the red card down if it did not fail to correspond with some image he had in mind, and why when he put the green up should he leave it up and go up on the high box for food if the green did not correspond with some image he had in mind?" It seems to the writer that the supposition of an image is unnecessary, except possibly in the experiments requiring discrimination of sizes. It is perfectly possible, as we know from our own experience, to react to one stimulus and not to another without going through a comparison of the two, unless the difference between them is merely one of degree. It might have been possible for a human being to discriminate between the larger and the smaller cards only by calling up a memory image of the card not shown and comparing it with the one before him; it surely would not have been necessary for him to use images in the reactions to colors, forms, and tones. And if a human being, accustomed to much dependence on memory ideas, could get on without them here, surely a raccoon could. Even in judgments of degree, all laboratory psychologists know that human beings have a strong tendency to make absolute rather than comparative judgments, and use memory ideas but little. Better, though still unsatisfactory, evidence of the use of images is furnished by the following method: "Three levers were placed on the displayer. One, on being raised, displayed white, another orange, another blue. The plan was to display white, orange, and blue consecutively, then to display the same blue three times. I fed the animal if he climbed upon the high box on being shown the series white, orange, blue, and did not feed him after the series blue, blue, blue." That is, the stimulus immediately preceding the reaction was the same in both cases. The difference lay in the foregoing stimuli. The series

"white. blue, red, food" and "red, red, red, no food" was also used. The raccoons learned to respond properly, "though," Cole continues, "I never *completely* inhibited the animals' tendency to start up on seeing white or blue, which were precursors of the red which meant food. Thus the animals all anticipated red on seeing its precursors, which in itself seems good evidence of ideation. Many times, however, they turned back after starting at blue or white and looked for the red, then climbed up once more, thus showing that the red was not a neglected element of the situation, but an expected color which they generally waited to see, but sometimes were too eager to wait for." Certain details of the raccoons' behavior are significant. "Each one, on seeing the first red, would drop down from a position with both front paws on the front board to stand on all fours in front of it, and merely glance up at the succeeding reds. As soon as the white appeared, however, the animal would lean up against the front board, claw down the white and blue, but *never the final red.*"

Now Cole thinks that the learning of this trick by the raccoons proved that "the animal *retains* an image of the cards which just preceded red." The only alternate supposition seems to him to be that they always reacted to the number of the card in the series, which, if the series were irregularly given, would not have been the same in successive trials. To suggest one's own interpretation of animal behavior that one has not seen, in the place of the experimenter's interpretation, requires some temerity, but to the present writer the most natural way of accounting for the raccoon's performances would be the supposition that in the series white, blue, red, for instance, at the end of which they were fed, the occurrence of white threw them into a state of expectancy, of readiness to climb up on the

box; this was heightened by the blue, and finally "discharged" into action by the red. During this process they may have had an *anticipatory* image of the blue and of the red, although there is no evidence that they did. But when the red came they did not stop to call up *memory* images of the preceding colors, and decline to act until they had assured themselves that those were blue and white instead of red. Preparedness to act was probably already secured by the actual occurrence of the white card at the beginning of the series. In other words, while images may have been present, they were images with a future, not a past reference. A human being reacting to a series of stimuli in this fashion would but rarely, in case his attention had wandered during the giving of the first two stimuli, have to recall them as memory images before reaction, but he might very likely have anticipatory images of the stimuli to come while waiting for them. These criticisms, which appeared in the first edition of the present work, were later repeated by Gregg and McPheeters (268 a), who made experiments similar to Cole's.

In favor of the functioning of ideas in monkeys and raccoons is the fact that in learning to open puzzle-boxes, they drop off useless movements with great speed. And monkeys have given clear evidence of inferential imitation. Kinnaman (401) reports that in one of his experiments, where the box had to be opened by pulling out a plug, a monkey failed to work the mechanism and gave up in despair. Another monkey then came out of the cage, the first one following. Number two went to the box, seized the end of the plug with his teeth, and pulled it out. The box was set again, and monkey number one rushed to it, seized the plug as number two had done, and got the food. She immediately repeated the act eight times. A second

and similar observation was made where the mechanism was a lever. Haggerty (281), as the result of long observation and experimenting on the monkeys in the Bronx Zoo, got some excellent instances of inferential imitation, of which one may be quoted. The act to be performed was that of climbing up the side of the cage, thrusting the arm up inside a wooden chute, and pulling a string inside it, as a result of which food came tumbling down. Monkey number 13 was allowed to watch monkey number 4 go through this process four times. "Number 4 was now removed and Number 13 was released in the cage. At first he looked about over the floor for food and then climbed the front wire, stopping on the brace opposite the chute. He leaned over to the chute and while still standing on the brace with his feet, tried to thrust a hand into the bottom of the chute. Failing in this, he ran along the brace . . . and back again to opposite the chute; catching the rung of the chute in his hands he drew himself over to it; finding himself above the end of the chute he tried to let his body down, first on one side and then on the other, until in the most awkward manner he managed to get near enough to the end to thrust a hand up the inside far enough to reach the string. At once he pulled and the food came tumbling down on his chest and to the floor. Dropping to the floor he picked up the food and ate it" (281, pp. 360-361). Such persistence of endeavor to carry out a definite act would certainly in a human being be guided by ideas.

Again, in Hunter's (350) work by the Delayed Reaction Method, the raccoons showed behavior which would seem to indicate the presence of a memory idea. Although they could not go in the right direction if more than twenty-five seconds had elapsed since the light was turned off,

they succeeded within this interval *whether they did or did not change the position of their bodies*. "Each of these animals could react successfully when the wrong orientation was held at the moment of release, and when, so far as the experimenter could detect, no part of the animal's body remained constant during the interval of delay" (p. 43). Thus, after the light was turned off, and they had moved about during the period of delay, when they were released they could move in the direction where they had seen the light. The same type of behavior, but extending over much longer periods of delay, was characteristic of children in similar tests, and would seem to be naturally accompanied by memory ideas, although Hunter prefers to speak of the re-arousal of "intra-organic cues." In the present writer's opinion, all ideas are accompanied by "intra-organic" or kinæsthetic cues. We shall refer later to this point.¹

Another experimental method which, like the Delayed Reaction Method, has been devised to study the possible functioning of ideas in various animals is the Multiple Choice Method. Its beginnings are to be found in the work of Hamilton (283). As he used it, the essential features were as follows. The animal was placed in a compartment with four exit doors. All of these doors were locked except one, and that one might be any one of the four except the door that was open in the previous experiment. The object of the test was to see whether or not the animal approached comprehension of this principle. The subjects were a normal man, a defective man,

¹ A curious type of delayed reaction, which must await further investigation, is reported by Mast (471) of the firefly *Photinus pyralis*. The flash of a female firefly causes the male to move in her direction. The turning of the male occurs *after* the female has flashed.

six boys of varying ages, one defective boy, five monkeys, sixteen dogs, seven cats, and a horse. Only the human subjects reached a stage of learning where they showed by their behavior that they realized the impossibility of opening a door that had been open in the preceding trial. The monkeys always tried all four doors, but did not often push repeatedly at the same door or persistently neglect a door; this lowest type of behavior was more frequent in the horse. The fact may be noted for future reference that the behavior of the horse in this situation was "stupider" than that of any of the other subjects.

Yerkes (826) developed the principle of this method and generalized it as follows. The animal is offered the choice among a number of compartments. The number can be varied, and their position in space can be varied. Thus, if there are ten compartments in the apparatus, only three of them may be used in a certain experiment, and these three may be situated in the middle or towards either end, so that no associations will be formed with position in space. Or in another experiment five of the compartments, in any part of the series, may be used. The compartments used in a given experiment have their entrance doors open. The problem may be varied in complexity by making the "right" compartment, the one whose entrance gives food, bear different relations to the rest. It may be the first compartment on the left, the first compartment on the right, the second on the left, the second on the right, the middle compartment, and so on. After an animal has proved its ability to learn a simple problem, such as "first on the right," it may be advanced to a more complex one, such as "second on the left." The method has been applied to crows (129), rats (113), pigs (826), monkeys, and apes (824). The crow mastered the "first at

the right" and "first at the left" problems, but failed in five hundred trials to master the "second at the left" problem. The white rat succeeded with the "first at the right," but failed with the "second from the left" problem. The pig distinguished itself by mastering "first at right," "second from left," "alternately first at left and first at right," failing only to grasp the "middle compartment" problem. The two monkeys tested by Yerkes (824) showed improvement in dealing with the problems "first at left," "second from right," "alternately first at left and first at right," and "middle," but appeared to owe many of their successes to their acquired preferences and aversions for particular compartments. The "alternating" problem proved to be especially easy. An orang-utan, who showed himself in other tests the most intelligent of Yerkes's subjects, failed to improve in solving the problems of the Multiple Choice Method. His wrong choices were so persistent, and so independent of the usual tendency to drop off useless movements, that Yerkes concluded him to be really acting on the basis of *wrong ideas* as to the correct solution of the problem. It is clear that a human being who had formed an incorrect theory as to the proper way to work out a problem would take longer to solve it than an animal who learned merely by the dropping off of useless movements, provided that the animal could solve it at all.

We may now examine the relation of the Multiple Choice Method to the question of the existence of memory ideas in animals. In the first place, if the "right" compartment always occupied the same position in space, clearly an animal might learn to go to it without the use of memory ideas. Kinæsthetic memory, the formation of a habit of turning in a certain direction, would suffice. Next, if the correct compartment is not always in the same absolute position

in space, but is always the furthest to the right or left of all the compartments used in the experiment, the learning is still easy. The animal has only to combine the habit of turning to the right or left with the observation as to what compartments have their entrance doors raised: a compartment with closed doors offers no stimulus. Thirdly, even the problem "second from the left," or right, might, it would appear, be solved without the use of a memory idea. The learning need involve only (a) the habit of turning to the left or right, and (b) the habit of reacting negatively to the open door furthest in this direction. The natural result of such a combined habit would be entering the door *next* to the end door. The problem of entering always the middle door of those open brings us closer to the use of memory ideas. An animal that had solved this problem would, on being confronted with the series of doors, find itself in an attitude representing a balance between the impulse of turning to the right and that of turning to the left. "Middleness" means a slight impulse to turn in one direction, offset by an equal impulse to turn in the other direction. Now the characteristic by which this situation differs from the other situations, involved in the simpler problems, is that the animal must not move at once, but must wait and assume the balanced attitude before moving. In the case of the other problems, he can start off immediately. Here an attitude must be revived before there is any actual movement. Just as in the Delayed Reaction Method success means, if the animal moves during the interval of delay, that it is able to revive an inner attitude which means motion towards the light, so here success means ability to revive an inner attitude which means movement towards the middle, a balance between right and left movements.

Further, what is the difference between reviving such a motor attitude at the sight of a stimulus, and making an ordinary response to a stimulus, such as any animal may learn? The difference is that in the latter case an actual, visible movement is made, while in the former case the movement is internally anticipated and not externally visible. Such an internally anticipated movement is probably always present when in the human consciousness we have a memory idea: when I recall a mental image of an object such as a fork, I "internally anticipate" the movements of handling the fork. Whether the converse of this proposition is also true, and we invariably have memory ideas whenever we internally anticipate movements, is highly doubtful, but at least it may safely be said that an animal which gives evidence of being able to anticipate its own movements has the possibility of memory ideas in its consciousness. (For reasons which have been elsewhere¹ stated, the present writer is inclined to think that this internal anticipation of movements means actual slight contractions of the muscles involved in performing the movements.) Whenever, then, as in the case of success in the Delayed Reaction Method where the bodily position is varied, in that of inferential imitation, and in that of choosing always the middle stimulus, the behavior seems to demand that the movements shall be anticipated by the animal which performs them, we have evidence in favor of the memory idea.

§ 78. *Conditions Favoring the Development of Memory Ideas*

An important condition of an animal's ability to anticipate its movements, to "know beforehand" what it

¹ Movement and Mental Imagery. New York, 1916.

is going to do, is obviously the ability to keep from actually reacting on the instant when the stimulus acts. To recall a memory idea, to anticipate by slight and invisible movements the response one is going to make, implies waiting a brief interval at least before making it in full. Now the development of sense-organs which can receive stimuli coming from a distance is an absolutely necessary prerequisite for the safety of delaying reaction. An important difference exists between the stimuli from objects directly in contact with an organism's body, such as in our own experience give rise to touch, temperature, pain and taste sensations, and those which proceed from objects at a distance, such as light, sound, and odors. This difference consists in the fact that the former have a more direct and instant effect upon the organism's welfare, and in consequence demand more rapid reaction than the latter. A stimulus in immediate contact with an animal's body may have a harmful or beneficial influence at the moment of its impact; it may be food to be seized or an enemy to be escaped, and the seizing or escaping must be done on the instant; on the other hand if an animal possesses the power, belonging in an increasing degree to animals as we go up the scale, of reacting to influences proceeding from objects still at a distance, it may safely delay its reaction when the stimulus is given. The danger is not so imminent, the food is not yet within reach; the full motor response to stimulation may be suspended for a short interval without imperiling the life interests of the animal. Thus one condition for the development and use of memory ideas is *the evolution of sense-organs for the reception of stimuli at a distance*. This idea was first suggested by the writer in 1904 (755); a similar conception, developed from the neurological standpoint, appears in Sherrington's

"The Integrative Action of the Nervous System" (681, pp. 324 ff.). Sherrington proposes the term "distance receptors" for those receptive organs "which react to objects at a distance," and declares that "the distance receptors contribute most to the uprearing of the cerebrum." The most important significance of the power to act in response to distant objects Sherrington finds to be that it allows an interval for preparatory adjustment, "for preparatory reactive steps which can go far to influence the success of attempts either to obtain actual contact or to avoid actual contact with the object." That these preparatory steps may also involve the germ of the memory image is clearly suggested by Sherrington. "We may suppose," he says, "that in the time run through by a course of action focussed upon a final consummatory event, opportunity is given for instinct, with its germ of memory, however rudimentary, and its germ of anticipation, however slight, to evolve under selection that mental extension of the present backward into the past and forward into the future which in the highest animals forms the prerogative of more developed mind. Nothing, it would seem, could better insure the course of action taken in that interval being the right one than memory and anticipatory forecast" (p. 332).

Secondly, if memory ideas depend on the anticipation of movements, during the delay between stimulus and full response, an important condition of their variety and free use is the *ability of the animal to perform a great variety of movements, and especially of movements other than those of locomotion*. Locomotion gets an animal into difficulties and rescues it; movements of locomotion are of the first practical importance. But they have not a great deal of variety. It is not merely a coincidence that the best

evidences of memory ideas should appear in animals which like the raccoon and the monkey are dexterous, able to use their paws for movements more complex and refined than those of locomotion. The supreme development of ideas comes in the mind of the animal which has not merely hands, but vocal organs, so that an infinite variety of delicate and complicated movements can be anticipated, and can form the basis of memory ideas.

Thirdly, one of the conditions of the anticipation of a movement appears to be attention to it when it is originally performed. In order to remember a movement, we must have paid attention to the sensations which its performance occasions, to the way it feels to make the movement. And one condition for attention to the way a movement feels is being comparatively safe from external dangers when the movement is made. An animal under ordinary conditions of wild life has very little attention to spare for his own movements. It would thus seem as though one requirement which must be fulfilled if anticipated movements are to play an important part in a creature's experience were that the animal should, for a time at least, be set free from the pressure of the practical hand-to-hand struggle for the means of existence, and thus enabled in safety to attend to its own movement sensations. Animal play, at first thought, offers an instance of such liberation from practical necessities. But as Groos has shown, animal play is not so unpractical as it looks (270). It is simply the exercise of the same instincts upon which in other circumstances the animal's welfare depends. The attention is absorbed in external objects quite as much in play as in the actual chase or warfare. The kitten watches the string, for which she has no practical use, as intently as she watches the bird for which she does

have a practical use; the dogs rolling over and over each other are nearly as absorbed in each other's movements as if they were in deadly combat.

That relief from practical necessity which will serve the purpose we are considering is to be found not in play, but in infancy. If a creature spends the period during which its nervous system is undergoing most rapid development in a state of complete shelter and protection from external danger, with all its vital needs supplied, then the nervous energy which under other conditions would be expended in the processes underlying attention to external stimuli is free to be so devoted that attention will be directed toward the creature's inner experiences. The human baby, while he may be interested in lights and sounds, in external impressions, does not need to be alert and watchful lest he miss his dinner or be dined on himself; his attention is free to be expended on his own movement experiences as well as on anything else. That young children do go through a stage of intense interest in the sensations resulting from their own movements is a fact made clear from many observations. The curious period of "self-imitation" in the child when it repeats for an indefinite period the same movement or sound, over and over again (14), is very likely a period of vivid attention to movement sensations.

That the prolonged period of human infancy is of advantage to the intellectual life of man because it means plasticity, the absence of fixed instincts that would take the place of acquisition by individual experience, was first pointed out by Fiske (227). But quite as important is the fact that in prolonged infancy we have the opportunity for acquiring the habit of that attention to our own movements which is the prerequisite for anticipated movements.

There are, as we have seen, various ways of learning by experience — slow ways that do not involve ideas, and the rapid way that does. The great advantage of man over most of the lower animals is not so much in the fact as in the method of his learning. One of the most vital meanings of the long period of helplessness and dependence constituting human infancy lies in the fact that by relieving from the necessity of attending exclusively to external objects, it renders possible attention to the sensations resulting from movement; and thus, by supplying an essential condition for the anticipated movements, it opens the way for the control of movement through ideas.

§ 79. *Some Alleged Instances of Remarkable Mental Powers in Animals*

All of the experimental evidence which we have examined indicates that even in the cleverest animals intellectual ability falls far short of that demonstrated by rather dull human beings. But a few years ago in Germany the hypothesis was advanced that the minds of such animals as horses and dogs are really quite on a par with those of human beings; their apparent deficiencies being due to the fact that we have never learned how to educate and communicate with animals. In 1901 a Berlin gentleman, Herr von Osten, began training a five-year old horse named Hans to answer arithmetical questions by tapping with his hoof on the ground. Taps with the right hoof meant units, taps with the left hoof meant tens. Later, an alphabetic system was constructed on a numerical chart: the letter *a*, for example, being found in the vertical column numbered 3 and the horizontal column numbered 2, tapping three times with the left hoof and twice with the right

meant *a*. Thus Hans was trained to answer questions other than those concerned with numbers. He showed ability to do so with seeming intelligence, and to work arithmetical problems. He was examined successively by two commissions, and a psychologist on the second commission, Pfungst, apparently solved the mystery of Hans's behavior by showing that the person who put the questions to the horse made unintentionally a slight movement of the head when the proper number of taps had been given, and that when such movements were intentionally made, the horse responded to them. So the matter rested, with the simple solution that the horse had, instead of really thinking, merely reacted to involuntary signals. After the death of Herr von Osten, Hans came into the possession of Herr Krall, a business man of Elberfeld, who was not satisfied with Pfungst's explanation, and besides continuing the education of Hans, trained several more horses, the most gifted of which were two Arabians named Muhammed and Zarif. In two weeks Muhammed learned to add and to subtract; he passed in three days from multiplication and division to the use of fractions; he acquired remarkable skill in the extraction of square and cube roots, and finally he as well as his fellow pupil began to offer original observations. These performances occurred even when the horses were prevented from seeing any one. Much the same sort of phenomena are reported in the case of Rolf, the Mannheim dog. The most recent reports of the Elberfeld horses are less enthusiastic, and even claim fraud, although not on the part of Herr Krall, whose disinterestedness seems accepted. It is impossible to determine just what cues are responded to by these animals in their performances, but aside from all the negative weight of the evidence obtained under exact experimental conditions on

other animals (it will be recalled that the horse was the stupidest of all Hamilton's subjects), certain indications point clearly away from the possibility that the horses are really mathematical geniuses. (1) They learn too quickly to allow of their understanding. A gifted human being could not acquire so fast a real apprehension of mathematical relationships. (2) They take no longer for hard problems than for easy ones. (3) They begin tapping without even glancing at the problem written on the board. (4) The character of the mistakes they make is not that of the mistakes of a real calculator: very common errors are reversals of the figures, thus 27 for 72, or errors of one unit, as 21 instead of 22. These are errors which might easily be made if the two forefeet were confused in the tapping, or if the tapping stopped a little too soon or not quite soon enough. They are not real arithmetical errors, such as forgetting to carry a figure over from one column to another, for instance. (4) No really satisfactory results have been reported when no one present knew the correct answer. On the whole, the phenomena do not present themselves with such authority as to compel a revision of our whole conception of the animal mind (125, 126, 200, 278, 383, 459, 460, 489, 511, 577 a, 653).

§ 80. *Certain Influences Affecting Learning*

We may conclude our study of the modification of conscious processes by individual experience with a brief summary of some incidental factors which affect the learning process. (1) The *age* of the animal has an influence upon its ability to learn. Watson (766) compared the ability of young white rats with that of mature animals in the learning of puzzle-box and maze habits. He was espe-

cially interested in testing Flechsig's theory that learning depends upon the presence of medullated fibres in the central nervous system. The theory was unconfirmed, for such medullation is highly imperfect in the rat at twenty-four days of age, yet at this age Watson's rats learned a labyrinth more quickly than did the adults. The rat belongs to the class of animals that are born unable to care for themselves, and before those observed by Watson had reached the age of twelve days, they were unable to find their way by a simple maze path back to the mother. The superiority of young rats over adults in learning a maze path is apparently due to their greater activity; they make more useless movements, and in solving a puzzle box they are at a disadvantage as compared with their elders.

Allen's (4) work on the guinea pig was intended for comparison with Watson's study, because the guinea pig comes into the world, not helpless like the baby rat, but well equipped on both the sensory and motor sides. In the labyrinth tests the mother was put at the end of the maze, and the sight and smell of her were supposed to serve as the stimulus to activity. Before the young animals reached the age of two days they did not succeed in learning a comparatively simple path, but at that age they did learn it, and proved the fact when the wire netting box in which they were placed was turned about, by pushing at the place where the opening had been. At three days they learned a more complex maze, and appeared to possess the learning capacity of adults.

Yerkes (821) found that the dancing mouse at one month old learns a black-white discrimination faster than an older mouse. From one to seven months of age there is a decrease in learning speed; from seven to ten months, an

increase. The power to discriminate appears to be better in younger mice; the power to associate better in older ones. Thus the superiority of the younger animals is rather in speed of sense perception and movement than in real learning ability.

Hubbert (345) has confirmed the statement that young rats learn the maze more rapidly than older ones. Moreover, she finds that in the younger animals, the most rapid stage of the learning occurs at an earlier point.

(2) The sex of the learner may have some effect on the learning, although no very definite differences have thus far appeared. Yerkes (821) reports that young male dancing mice learn faster than females, and that females from four to ten months of age learn faster than males. Hubbert (345) states that except in the cases of very young and very old rats, males learn more readily than females; the absolute time of running the maze is however shorter for females.

(3) The number of trials a day affects the speed of the learning. Yerkes (820) found that the dancing mouse learned a white-black discrimination in fewer trials the smaller the number of trials a day. Ulrich (738) has shown that the white rat learns a puzzle-box habit or a maze habit in fewer trials if one trial is given a day than it requires if either three or five trials are given a day. Apparently even better results are secured by one trial every third day. The same principle appeared to hold when several problems were being learned at once. This principle, known as that of distributed repetitions, has long been recognized in human memorizing, although we do not know the explanation for it. But learning is always more economically secured if intervals of time are allowed to elapse between repetitions.

(4) The learning of one habit may influence the later

acquisition of other habits. Yerkes (820) reports that dancing mice which have learned one maze learn another one more readily than those which have had no previous training. Richardson (634) finds previous experience a help also to the rat: experienced animals were more susceptible to stimuli and showed better coördination of their activities. Hunter (349), on the other hand, found that pigeons which had learned one maze were delayed in learning a second one, and Yoakum (832) reports a similar condition in the learning of puzzle-boxes by squirrels: the older habits interfere with the acquisition of the newer ones. Hunter and Yarbrough (355) conclude from experiments on establishing auditory associations in white rats that a formed habit interferes with the formation of a new one, but that the new habit does not react unfavorably upon the old one. This has been found true of human memorizing also. Probably, when an animal seems to learn a new habit better because of having previously formed a different habit, the advantage is merely in the fact that it has become used to being experimented upon, to the experimental situation.

(5) The differences in individual ability among animals are marked. We are inclined to think of all the animals of a certain species, especially if it be a species far removed from man, as equally gifted, but it is quite possible that among ants and earthworms there are geniuses and dunces. Turner (729, 730) reports striking individual variations in the behavior of cockroaches learning a maze; two of the rats tested by Small (685) with puzzle-boxes never learned to get into the boxes, but merely profited by the activity of their more gifted companions. Wodsedalek (795) gives a delightful account of a specially talented Mayfly. Practically every experimenter reports similar individual variations.

CHAPTER XII

SOME ASPECTS OF ATTENTION

THE student absorbed in reading "does not hear" an approaching footstep. That is, a stimulus which would under other circumstances produce an effect loses a great part of its influence because of the fact that another stimulus is already upon the field. This other stimulus need not be more intense, that is, need not involve more physical energy, than the one which is ignored. It does not win the victory by a mere swamping of its rival through its superior quantity. A man may walk along city streets, his eyes and ears bombarded with brilliant lights and loud sounds, and yet the centre of his consciousness may be a train of ideas, representing in their physical accompaniment in his cortex a quantity of energy insignificant compared with that of the external stimuli pouring in upon him. Psychologists commonly express this fact by saying that while the strength of a stimulus conditions the intensity of the mental process accompanying it, the *clearness* of that process depends upon *attention*.

§ 81. *The Interference of Stimuli*

Attention, then, is the name given to a device, whatever its nature, whereby one stimulus has its effectiveness increased over that of another whose physical energy may be greater. What happens in the simpler forms of animal life when two stimuli, requiring different reactions, operate

simultaneously? We may quote from Jennings the facts about *Paramecium*. "If the animal is at rest against a mass of vegetable matter or a bit of paper, . . . and it is then struck with the tip of a glass rod, we find that at first it may not react to the latter stimulus at all." "A strong blow on the anterior end causes the animal to leave the solid and give the typical avoiding reaction." "If specimens showing the contact reaction are heated, it is found that they do not react to the heat until a higher temperature is reached than that necessary to cause a definite reaction in free-swimming specimens." "On the other hand, both heat and cold interfere with the contact reaction. *Paramecia* much above or much below the usual temperature do not settle against solids with which they come in contact, but respond instead by a pronounced avoiding reaction." "Specimens in contact with a solid react less readily to chemicals than do free specimens. . . . On the other hand, immersion in strong chemicals prevents the positive contact reaction." "The contact reaction may completely prevent the reaction to gravity," and to water currents. It also modifies the reaction to the electric current. While a part of the influence exerted by the contact reaction on other responses may be purely physical, due to the fact that an actual secretion of mucus may occur whereby the animal "sticks fast" to the solid, yet this alone does not explain the facts, for the cilia that are not attached do not behave normally. The reaction to gravity regularly yields whenever opposed to the action of any other stimulus (378, pp. 92 ff.).

Sometimes the action of one form of stimulation merely affects the form of the response to another, as in the case where abnormal temperature causes the avoiding instead of the positive reaction to be given to solids. In other cases, reaction to one of the stimuli is suppressed or weakened.

The facts suggest that the influential stimulus is either the *one that is on the field first* (the contact reaction may prevent response to temperature, or abnormal temperature may modify the contact reaction), or the *one that is the more important* (gravity yields always to other stimuli).

In some higher animals the effects of interference of stimuli have been noted. The earthworm will not respond to light if feeding (171) or mating (327). In the turbellarian *Convoluta roscoffensis* light is victorious over heat in determining reaction. The animals in their positively phototropic phase will remain in the heated light end of a vessel until they perish. Light and gravity are more nearly balanced in their effects. *Convoluta* is negatively geotropic, yet if the brightest region is below the surface, the animals will go there. But if this region is only a little brighter than the surface, they will stay at the surface, gravity dominating (253). The sea-urchin shows in its behavior a somewhat similar relation between mechanical and chemical stimulation. If weak acid is dropped into the water containing specimens of *Arbacia*, their spines begin to interlace. A slight shaking will restore them to the normal position, but if more acid be added, no mechanical stimulation will overcome the effect of the chemical (734). Various facts concerning the interrelations of gravity and light as stimuli have been noted in Chapter IX. A very interesting case of the suppression of one reaction by another is reported by Holmes in his observations on the water insect *Ranatra*. The positive response of this insect to light, very precise and striking, may be wholly suspended when the animal is feeding, when a number of individuals are collected, when the insect stops to clean itself, or even "by the sudden appearance of a large object in the field of vision," behavior which is strongly

suggestive of the "distraction of attention" in a human being (335). Holmes (337) also observed that the fiddler crab, although it ordinarily moves towards the light, would run away from a moving light, fear overcoming positive phototropism. Roubaud, in a study of the behavior of some species of flies that live on the seashore, feeding on dead fish and the like, says that they will abandon the "head on" position which they regularly assume toward the wind, if attracted by the odor of food (646).

Wherever we find that one class of stimuli regularly yields to another if the two act together, it is safe to assume that the prepotent stimulus is more important to the organism's welfare than the vanquished one. And while we cannot without more ado call such cases of the interference of stimuli as are found in very simple animals cases of attention, and ascribe to their psychic accompaniment all the characteristics of attention as a feature of our own experience, yet we may assert that they have in common with attention the significance of being *a device to secure reaction to the most vitally important of several stimuli acting at once upon the organism.*

§ 82. *Methods of securing Prepotency of vitally Important Stimuli*

An inanimate object acted upon by several forces at once is determined in its motion by their relative intensity. Conceivably, an extremely simple form of animal life, when subjected to two stimulations acting together, would also respond in a way answering precisely to the relative strength of the two. It is easy to see what would be the disadvantage of such a state of affairs for the animal. The weaker of the two stimuli might be of far greater significance for

organic welfare than the stronger. For example, it would often be important that an animal should be able to respond to a very faint food stimulus rather than to any of the stronger forces acting upon it. Evidently a prime need of animal life is some arrangement whereby weak but important stimuli shall be given the preference in determining reaction over stronger but less vitally necessary ones. *Sense organs* are one such device. The comparatively slight amount of chemical energy coming from a bit of food may have its effectiveness for the nervous system greatly increased through its reception by a structure adapted to use the whole of it to advantage. Light stimulation involves a quantity of energy that is insignificant in comparison with the grosser forces acting on an organism; yet falling on the retina, the energy is economized and magnified through the stored-up chemical forces it sets free. Thus a weak stimulus may by a sense organ be made powerful to determine reaction. Another arrangement to the same effect is the peculiarity of the nervous system whereby, through an arrangement akin to the summation of faint stimuli, a *moving stimulus*, one acting successively upon neighboring points of a sensitive surface, *produces an effect disproportionate to its intensity*. A moving stimulus is a vitally important stimulus; it means life, and hence may mean food or danger. The response to it is in most cases adapted rather to its importance than to its physical strength. A third arrangement for the securing of reaction to vitally important stimulation lies in the existence of *preformed connections* in the nervous system, which bring it about that the *path of the excitation produced by one stimulus is clear to the motor apparatus*, while that of another is closed. Reactions of this sort we call instinctive. The nesting bird responds to the sight of building material rather

than to that of objects offering equally strong stimulation to the optic nerve; the cat sits at the mouse hole, the parent animal responds to the faintest cry of the offspring, because these stimuli have the right of way by virtue of inherited nervous connections.

Finally, a weak stimulus may determine reaction and be victorious over a stronger one because of *nervous pathways formed through the individual's own experience*. The consequences of reaction to it in the individual's past may operate to secure reaction to it in the future. To the cat in a puzzle box, the string that must be pulled to let it out offered originally no stronger stimulus to action than any other object in sight; but after sufficient experience the string comes to dominate the situation and determine the cat's behavior. If the experience of consequences is slowly acquired, by many repetitions, the process of reacting to an object originally indifferent may be unaccompanied by any ideas of the consequences of such reaction. If it is rapidly acquired, we know that we human beings at least accompany our reactions by calling up the results of our past reactions in the form of memory ideas.

§ 83. *The Peculiar Characteristics of Attention as a Device to Secure Prepotency*

We have suggested that attention is a means of securing reaction to the vitally important stimuli acting upon an organism. Does reaction to a stimulus always mean attention to the sensation accompanying that stimulus?

This question may best be answered by examining the characteristics of the attention process as we know it. In attention, the details of the object attended to become clear and distinct. That is, attention is a state where discrimina-

tion is improved. Further, attention involves varying degrees of effort, and these are marked by varying intensity of certain bodily processes. Attention under difficulties is accompanied by a rigid position of the body, by holding the breath, and by various muscular effects, aside from the processes which, like frowning, are concerned with the adaptation of the sense organ to receive an impression. These general bodily effects of attention are all such as to suggest that the body is to be kept as quiet as possible during the attentive state. In other words, no reaction is to be made to the object attended to except such as may be necessary to allow its being carefully discriminated from other objects. *Attention, in its intenser degrees, at least, seems to involve a state of suspended reaction.*

Not every case, then, of response adapted to the vital importance of a stimulus is a case that suggests as its psychic aspect attention to the accompanying sensation. When, for example, a reaction of especial speed is made to contact with a moving stimulus, the speed of the reaction would itself indicate that the sensations produced are not attended to. The proper situation for attention would be the situation in which the reaction needs to be suspended until the stimulus is fully discriminated. Now such careful discrimination does not appear to be characteristic of reactions that are largely based on inherited nervous structures. Many facts concerning the instincts of animals, that is, their inherited reactions, indicate that these are extremely rough adjustments of behavior to environment until refined by individual experience. Hudson observed, for example, that newly born lambs on the South American plains had a tendency to run away from any object that approached them, and to follow any object that receded from them. They would follow his horse for miles as he rode along, and would run

away from their own mothers when the latter moved toward them. He explained this as adapted to the fact that ordinarily their first duty, on making their appearance in the world, is to keep up with the receding herd, while an approaching object is more likely to be an enemy (347). Later, this rough adjustment is modified; they learn by experience not to run away from their mothers, and not to follow indiscriminately any leader.

If it is true that instinct unmodified by experience is adapted to general rather than to special features of environment, it seems likely that the phenomena of attention as we know them are found chiefly in connection with those responses to vitally important stimulation which are determined, in part, at least, by the individual experience of the reacting animal, for these are the responses requiring most careful discrimination among stimuli, and the delay of reaction until such discrimination has been made.¹ Putting the matter in a slightly different way, we may say that purely inherited responses can be adapted only to certain broad, roughly distinguished classes of stimuli, for these alone are common to the experience of all members of the species. Nothing but individual experience can bring to light the importance for welfare of certain particular stimuli, for the significance of these would vary with the experience of each individual animal. Among the lower animals, attention probably reaches its highest pitch where the response most needs to be suspended in order that the

¹ In this connection Franz's experimental demonstration that the frontal lobes, long regarded as the seat of the neural processes underlying attention, are concerned in the functioning of recently learned reactions, is of especial interest. Franz found that cats and monkeys which had been trained to work mechanisms lost the power to do so when the frontal lobes were extirpated, although habits of older date, such as responding to a call, were preserved (237, 238).

stimulus may be fully discriminated. The rabbit or wild bird crouching motionless close to the ground, watching each movement of a possible enemy, suggests strongly to our minds a condition of breathless attention. Whether such an interpretation is the true one depends very much, I should say, on the extent to which past individual experience has refined the animal's powers of discrimination. Mere "freezing to the spot" may be an inherited reaction, useful in time of danger, but more analogous in its psychic aspect to the blank emptiness of the hypnotic trance than to alert, watchful attention.

Yet although, in so far as attention is a state favoring discrimination of stimuli, it is involved in that part of an animal's behavior which is derived from individual experience, since pure instinct discriminates but roughly; in so far as it is still one of the devices for securing reaction to stimuli of vital importance, its root must lie in instinct. No object wholly unrelated to some fundamental instinct can hope to secure attention, for the great classes of vitally important stimuli have all of them preformed paths in the nervous system by which their reactions are secured. What individual experience does is to refine upon the adaptations which instinct makes possible; to bring about the connection of certain stimuli, originally indifferent, with the performance of an instinctive response, or to produce a checking of the instinctive response when certain individual peculiarities of a stimulus that would otherwise call it forth become evident. For instance, an animal learns by experience to come at the call of a human being who feeds it; the sound, originally without effect on its reactions, has come to be connected with the nervous mechanism of an instinct. The chick pecking at small objects on the ground learns by experience to inhibit this instinctive response with

reference to objects having certain peculiarities originally undiscriminated, but now in some way emphasized through painful circumstances accompanying his previous encounter with them.

The most fundamental characteristic of attention, then, is perhaps that aspect of it which has been called *abstraction*, the diminished effectiveness of stimuli not attended to. By virtue of this aspect we recognize that attention belongs with instinct as being concerned in securing the prepotency of vitally important stimulation. On the other hand, the further characteristic of attention; namely, that it is a state of suspended reaction involving careful discrimination of stimuli, suggests that its functioning is connected rather with the refining and modifying influence of individual experience acting on instinct, since here alone do we find delayed reaction and accurate stimulus discrimination.

The highest grade of attention, the final triumph of vital importance over mere intensity of stimulation, is to be found where the focus of attention is occupied by an idea or train of ideas. When a process purely centrally excited holds the field and makes the individual deaf and blind to powerful external stimuli pouring in upon his sense organs, then he is superior to the immediate environment at least. This form of attention occurs, probably, only when the vital importance of the idea attended to has been learned through that most rapid form of individual acquisition of experience which involves the revival of the past in idea. It has been called derived attention. The ideas attended to are held in the focus of consciousness and analyzed through the power of associated ideas. The inventor holds to his problem, the student to his task, in spite of distractions, because of the consequences which he thinks of as likely to result. It seems unlikely that attention in this final form occurs among

the lower animals. While ideas are probably present to some extent in the minds of the higher mammals, they are hardly so far freed from connection with external stimuli that the animal can shut out the world of sense from its consciousness and dwell in a world of ideas.

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